ce Library JAN 4 1945

Vol. 72 JANUARY-FEBRUARY, 1945 No. 1

Bulletin

of the

Torrey Botanical Club

Editor
Harold W. Rickett

Associate Editors

Irving W. Bailey
Edward W. Berry
Stanley A. Cain
M. A. Chrysler
Harold H. Clum
Adriance S. Foster
Henry Allan Gleason
Arthur H. Graves
John W. Shive
R. P. Wodehouse
Michael Levine

CONTENTS

Vaccinium Hybrids and the Development of New Horticultural Material ..... *George M. Darrow and W. H. Camp* 1

Dryopteris, Deschampsia, Portulaca, Lupinus, Fagara, Stenogyne, and Dubautia. Hawaiian Plant Studies 12 ..... *Harold St. John* 22

The Jatrophas of Cervantes and of the Sessé & Mociño Herbarium. *Rogers McVaugh* 31

Juniperus virginiana, J. horizontalis, and J. scopulorum—III. Possible Hybridization of J. horizontalis and J. scopulorum. *Norman C. Fassett* 42

Rhizidiomyces hirsutus Sp. Nov., a Hairy Anisochytrid from Brazil. *John S. Karling* 47

History and Nomenclature of the Higher Units of Classification. *Leon Croizat* 53

Effect of Cotton on the Germination of Phycomyces Spores. *William J. Robbins and Mary Bartley Schmitt* 76

A Morphological and Cytological Study of a New Form of Volvox—I. *Jerome Metzner* 86

Index to American Botanical Literature 114

Published for the Club bi-monthly
by
THE SCIENCE PRESS PRINTING COMPANY
N. QUEEN ST. AND McGOVERN AVE.
LANCASTER, PENNSYLVANIA

'45

THE TORREY BOTANICAL CLUB

Officers for 1944

President: MICHAEL LEVINE

Vice-presidents: FRED J. SEAVER, HENRY K. SVENSON

Recording Secretary: HONOR M. HOLLINGHURST

Corresponding Secretary: EDWIN B. MATZKE

Treasurer: PAGE J. KARLING

Editor: HAROLD W. RICKETT

Business Manager: HAROLD H. CLUM

Bibliographer: MRS. LAZELLA SCHWARTEN

For information about the publications and proceedings of the Club, and about membership, dues, and meetings, see Torreya, published quarterly by the Club.

The Bulletin of the Torrey Botanical Club

Subscriptions, dues, and inquiries about back numbers should be sent to the office of publication, N. Queen St. and McGovern Ave., Lancaster, Pa., or to Page J. Karling, Department of Botany, Columbia University, New York 27, N. Y. Correspondence about advertisements and circulation should be addressed to Dr. Harold H. Clum, Hunter College, New York 21, N. Y. Communications about exchanges should be sent to Dr. Edwin B. Matzke, Department of Botany, Columbia University, New York 27, N. Y. Manuscripts intended for the Bulletin should be sent to Dr. H. W. Rickett, The New York Botanical Garden, New York 58, N. Y.

Claims for missing numbers must be made within 60 days from the date of issue.

The subscription price of the Bulletin of the Torrey Botanical Club is $6.00 a year except to active members of the Club. Of the annual membership dues, $3.00 covers a year's subscription to the Bulletin.

Torreya. Quarterly; established 1901. Of the annual dues $0.50 is for a year's subscription to Torreya; price to non-members, $1.00.

Entered as second-class matter October 8, 1940 at the post office at Lancaster, Pa., under the Act of March 3, 1879. Accepted for mailing at the special rate of postage provided for in the Act of February 28, 1925, embodied in paragraph 4, section 538, P. L. & R.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 72, NO. 1, PP. 1–21 JANUARY, 1945

VACCINIUM HYBRIDS AND THE DEVELOPMENT OF NEW HORTICULTURAL MATERIAL

GEORGE M. DARROW AND W. H. CAMP[1]

There is every evidence that the indigenous Americans made considerable use of blueberries (*Vaccinium* spp.) as food (5, p. 585–588), and some Esquimo tribes to this day pick the fruit of *V. uliginosum* L., place it in skin bags and store these bags of blueberries in holes in the ground in contact with the permanently frozen zone. This apparently is a forerunner of our present out-of-season frozen "consumer package," a delicacy becoming more common on our own tables each year. The early settlers from Europe were not long in discovering this delectable addition to their fare. That the popularity of the blueberry is well deserved is indicated by the fact that, currently, a crop of a value ranging from $5,000,000 to $10,000,000 is harvested annually in the United States from wild, semi-wild, and cultivated plants. This is in addition to a widely cultivated member of the same group, the American cranberry [*Oxycoccus macrocarpus* (Ait.) Pers. (= *V. macrocarpon* of some authors)].

The blueberries are a polymorphic group of plants. Some species form large bushes (records of 20 feet high being common), while others under no circumstances exceed a stature of 15 inches. Some species produce few stems, some many stems from a common base, while others regularly form from small to extensive colonies by means of underground stolons. By using a leaf abnormality as indicator, one such colony has been traced and found to be at least a half-mile in diameter. From the standpoint of their horticultural development, other characteristics of importance are the marked differences between species in drought resistance, winter dormant period, size, flavor, and color of the fruit, keeping quality of the fruit (which is influenced by several anatomical features), the size and shape of the flowers, and the size of the seed. Apparently minor items may be exceedingly important; for example, because of the size and shape of the flowers not all blueberry corollas are equally accessible to the various species of wild and domestic bees whose visits are necessary for pollination and consequent fruit production. Such things must be taken into account in a breeding program.

Hybridization in our cooperative work on *Vaccinium* has a rather wide application. In the first place, it is the only means whereby the numerous divergent characters of the various species may be combined to produce the desired forms for further breeding and for the selection of new horticultural

[1] Senior pomologist, Division of Fruit and Vegetable Crops and Diseases, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Administration, U. S. Department of Agriculture; and the New York Botanical Garden, New York, N. Y., respectively.

varieties. It is also an index of the ease with which interspecific hybrids may occur in nature and serves to explain many of the aberrant forms found in the wild. Moreover, it serves as a background for the study of the origin and nature of the various polyploid complexes found in the group.

HYBRIDS FROM CONTROLLED CROSSINGS

In this phase of the work the parent materials were brought into the experimental plots and greenhouses at Beltsville, Maryland, where the controlled crosses were made. The seedlings were grown in the greenhouse until ready to be set in the field test plots. Because the climate at Beltsville is not suitable for all species, especially those from the extreme South or North, extensive trial plots have been established at various places in New Jersey, Maryland, North Carolina, South Carolina, Georgia, and Louisiana, with smaller plots in other States.

To indicate something of the amount of material on which we have worked, in the years 1941, 1942, and 1943 approximately 18,000 plants from controlled crossings have been placed in the various test plots. The foregoing figure by no means represents the number of plants produced from controlled crossings—even during these 3 years. A complete genetic analysis of the material would necessitate that every effort be made to bring all members of a progeny to maturity for study. This, unfortunately, it has been impossible to do. In the first place, the nature of the project is such that rigid selection of the material must be practiced, even in the early stages of the plant's development and, therefore, individuals that did not meet certain horticultural standards were discarded almost immediately. Secondly, our facilities have limited the amount of material which could be handled, and plants have been discarded merely because of lack of space. However, efforts have been made to save as many types as possible as a basis for future work.

The following list, therefore, is merely an extract from the results of the work, indicating only the successful interspecific hybrid combinations produced under controlled conditions. To our own list have been added a few combinations previously reported by Coville (4) or known to have been made by him, the only change being that, in several instances, his nomenclature has been altered so as to coincide with ours.

Crosses between Diploids[2]

V. tenellum × *darrowi*
V. pallidum × *myrtilloides*
V. pallidum × *atrococcum*

[2] Although there is disagreement among systematists on whether *Polycodium* should be treated as a separate genus or as a subgenus of *Vaccinium*, it is of considerable interest to note that Coville was able to produce viable hybrids between *Polycodium stamineum* (L.) Greene and *Vaccinium myrtilloides* Michx., both diploids. Since one parent is a deerberry and not a blueberry, this hybrid is omitted from this list. His records and specimens indicate that he also made a successful cross between *Polycodium melanocarpum* and *Vaccinium myrtilloides*.

Crosses between Tetraploids

V. corymbosum × *virgatum*
V. australe × *simulatum*
V. australe × *tallapusae* (= *alto-montanum*)
V. australe × *myrsinites*
V. lamarckii × *tallapusae* (= *alto-montanum*)
V. lamarckii × *virgatum*
V. lamarckii × *hirsutum*
V. lamarckii × *brittonii*
V. lamarckii × *myrsinites*
V. australe × *virgatum*
V. australe × *lamarckii*
V. australe × *corymbosum*
V. australe × *hirsutum*
V. australe × *arctostaphylos*[3]
V. brittonii × *myrsinites*
(*V. lamarckii* × *australe*) × *virgatum*
(*V. lamarckii* × *myrsinites*) × *australe*
(*V. lamarckii* × *australe*) × *myrsinites*

Crosses between Hexaploids

V. ashei × *amoenum*
V. ashei × *constablaei*

Heteroploid Crosses

V. angustifolium (2x) × *tallapusae* (4x) (= *alto-montanum*)
V. australe (4x) × *amoenum* (6x)
V. australe (4x) × *ashei* (6x)
V. australe (4x) × *constablaei* (6x)
V. simulatum (4x) × *ashei* (6x)

There is also on hand a fairly large amount of cleaned and prepared seed from the 1942 and 1943 crosses. It is our experience that plump seed generally indicates the presence of viable embryos and successful germination though not necessarily fertile hybrid plants. The following list, therefore, indicates possible additional successful interspecific combinations.

Seed Obtained from Diploid Crosses

V. myrtilloides × *tenellum* (seed germinated)
V. myrtilloides × *pallidum*
V. myrtilloides × *elliottii*
V. darrowi × *elliottii* (seed germinated)
V. darrowi × *pallidum* (seed germinated)
V. darrowi × *ovatum*[4] (seed germinated)

Seed Obtained from Tetraploid Crosses

V. lamarckii × *arkansanum*
V. myrsinites × *arkansanum*
V. tallapusae (= *alto-montanum*) × *virgatum* (seed germinated)

Seed Obtained from Heteroploid Crosses

V. darrowi (2x) × *australe* (4x)[5]

[3] Of considerable interest because *V. arctostaphylos*—a species native in the Caucasus of Asia Minor—is generally placed in a section of the genus quite apart from *V. australe*.

[4] *V. ovatum* is an evergreen species of the West Coast of North America; *V. darrowi* is also evergreen. No plants have resulted from previous crosses involving *V. ovatum* with other species.

[5] We await the mature plants of this cross, as well as of *V. angustifolium* × *tallapusae* (= *alto-montanum*) of which we have a few plants, with considerable interest so that morphological and cytological examinations may be made. Pentaploids are produced with ease and have been found in the wild. Thus far, triploid plants are unknown. It is to be noted that this particular diploid × tetraploid cross yielded only about 20 seed, whereas the tetraploid × hexaploid combinations were generally much more successful, in one instance (*V. virgatum* × *ashei*) yielding a harvest of approximately 5,000 seed.

V. tallapusae (4x) × *ashei* (6x)
V. australe (4x) × *constablaei* (6x)
V. virgatum (4x) × *ashei* (6x)
[*V. australe* (4x) × *ashei* (6x)] (5x) × *ashei* (6x)
[*V. australe* (4x) × *ashei* (6x)] (5x) × *australe* (4x)
V. lamarckii (4x) × *ashei* (6x)
V. myrsinites (4x) × *ashei* (6x)
V. myrsinites (4x) × *constablaei* (6x)

HYBRIDS OBSERVED IN THE WILD

It is not always safe to assume that plants exhibiting the characters of two other species are hybrids; they may be part of a highly segregative allopolyploid population. This has been discussed elsewhere in a consideration of the genetic structure of the allopolyploid species (3, p. 342–346, 363, 364). Yet those who are reasonably familiar with the material, and are aware of the pitfalls, may often distinguish between hybrids and allopolyploid populations with some degree of accuracy. In our joint field work we have repeatedly noted individuals and communities which apparently were of hybrid and segregate origin, possessing characters of two species which, in that region, made distributional contact. Some of these hybrid combinations will be noted here, with a brief discussion of each. It should not be assumed that many of the hybrid plants are F_1. In fact, they are back-cross and segregate plants of diverse inheritance.

Diploid Hybrids

V. ELLIOTTII × DARROWI. The mayberry, *V. elliottii*, is somewhat variable, one of its phases (for example) having leaves that are reduced in area, relatively narrower, and more indurated than is typical; they are also inclined to be tardily deciduous. The observed hybrids indicate that this combination is very likely to have been the source of such aberrancies, since *V. darrowi* is small- and narrow-leafed, and evergreen. Nearly intermediate plants (possibly F_1) are essentially evergreen.

V. ELLIOTTII × ATROCOCCUM. Typically *V. elliottii* is glabrous; where its leaves are more or less pubescent, this pubescence, to a considerable extent, seems to have come from *V. atrococcum*. In the same areas where this variation occurs, the characters of *V. atrococcum* also are often blurred, the plants becoming more like *V. elliottii*.

V. TENELLUM × DARROWI. Apparently locally common. *V. tenellum* is glandular and deciduous, whereas *V. darrowi* is eglandular and evergreen. When experimentally produced from material typical of each species, some F_1 plants are glandular and completely evergreen and in these (and other) characters scarcely to be distinguished from the well-known *V. myrsinites*, a segregative tetraploid. If plants taken casually from the wild are used as parental material, the resulting progeny may vary toward one or the other parental type, indicating that these species—as taxonomic units—are not genetically pure.

V. TENELLUM × PALLIDUM and V. TENELLUM × VACILLANS. As will be noted in a later paper of this series, there are areas where *V. pallidum* and *V. vacillans* have hybridized, producing more or less blended populations. However, in certain areas in the Southeast, on the outer Piedmont and on the boundary between the Piedmont and Coastal Plain, material apparently rather typical of *V. pallidum* may be found. Where present in the same areas with *V. tenellum*, the two hybridize. Plants more closely related to *V. vacillans* are also present in this same general region; these too hybridize freely with *V. tenellum*. From the appearances of the wild populations, and the evidences of gene-exchanges, it would seem that these species are particularly adapted to genetic studies.

V. ATROCOCCUM × DARROWI. It is seldom that these two species appear in the same habitat; yet, where they do, most unusual series of plants result. One such community was found to run the gamut of variation between these two widely contrasting species—that is, highbush to lowbush, few stemmed to extensive colonies, macrophyllous to microphyllous, pubescent to glabrous, deciduous to evergreen, etc.

V. ATROCOCCUM × VACILLANS. An exceedingly common combination, producing—by segregation and genic infiltration—highly polymorphic populations, one of which has been described in some detail in another place (3, pp. 360–362). Wild plants have now been examined and prove to be diploid. Segregates of this combination have been described as *V. vacillans* var. *crinitum* Fernald. Populations described as *V. margarettae* Ashe and *V. missouriense* Ashe also seem likely to prove to be segregates from this combination.

V. ATROCOCCUM × CAESARIENSE. This combination is relatively common in certain areas along the eastern Coastal Plain, and the populations of both species give evidence of having exchanged genes.

V. TENELLUM × ELLIOTTII. Where these two come together, numerous colonies have been found that exhibit a variety of segregate characters derived from both species. Plants from the wild have been found to be diploid. Material much like this was the basis of *Cyanococcus cuthbertii* Small [= *Vaccinium cuthbertii* (Small) Uphof]. The type sheet is a mixed collection, but appears to be this combination (see next paragraph).

V. TENELLUM × CAESARIENSE. A considerable number of plants, probably of this combination, are known. A series of herbarium specimens was included by Small in *Cyanococcus cuthbertii;* it seems to have contained material of this and of the preceding combination, its polymorphic nature being held together—in definition—on the basis of the characters derived from the common ancestor, as well as the circumstance that both of the other ancestral species are highbush. The *V. tenellum* × *elliottii* combinations are easily separated from those of *V. tenellum* × *caesariense* if one looks for the sur-

viving characters in the combinations which serve to distinguish *V. elliottii* from *V. caesariense*.

V. CAESARIENSE × DARROWI. Evergreen plants, 1–2 meters high, have been found in northern Florida that would seem to be this combination. Several that have been examined have proved to be diploid.

V. ANGUSTIFOLIUM × MYRTILLOIDES. Apparently rare; but the increase of pubescence in *V. angustifolium* in areas where these species make contact, together with a partially serrulate condition in the otherwise entire leaf of *V. myrtilloides* (coupled with a loss of some pubescence), leads to the conclusion that natural hybrids do occur.

V. ANGUSTIFOLIUM × VACILLANS. Reciprocal morphological disturbances are to be noted where they make distributional contact. These disturbances are considerably more pronounced in *V. vacillans* than in *V. angustifolium*. Today, *V. vacillans* is invading the southern part of the range of *V. angustifolium*, in which this latter species is generally represented only by residual (and often ancient) clones which, of course, exhibit no evidence of the part they have played in the production of sometimes confusing plants. *V. dobbini* Burnham appears to have been described from plants of this combination; derived allotetraploids may also be present.

V. MYRTILLOIDES × ATROCOCCUM. The northern margin of the range of *V. atrococcum* slightly overlaps the southern margin of the range of *V. myrtilloides*. Being more or less confined to boggy areas in these two extremes of range, they make contact in certain localities. Where this happens, plants clearly intermediate in character may be found.

V. ANGUSTIFOLIUM × CAESARIENSE and V. ANGUSTIFOLIUM × ATROCOCCUM. "Halfhigh" plants, presumably of these combinations, have been found with the parents. Too often, however, the analysis is complicated by the presence of the tetraploids *V. corymbosum* and *V. lamarckii* in the same habitat; these also yield halfhigh plants with very similar characters, as will be noted in a later paragraph.

Tetraploid Hybrids

V. MARIANUM × AUSTRALE. Along the eastern Coastal Plain south of the glacial boundary, areas may be found where *V. marianum* occurs with *V. australe;* there the usual homogeneity of *V. australe* is disturbed, and it is concluded that this is the result of gene-exchange with *V. marianum*. This whole situation will be taken up in more detail in a later paper of this series.

V. BRITTONII × LAMARCKII. Although morphologically quite similar and long confused in herbaria, *V. brittonii* has glaucous leaves and twigs, and black fruit, whereas *V. lamarckii* has bright green, nonglaucous leaves and twigs, and glaucous fruit. Where these two chance to meet, plants are found that have reciprocal segregate characters. The two species hybridize easily under controlled conditions.

V. CORYMBOSUM. Our analysis of the polymorphic, tetraploid highbush population north of the glacial boundary—treated as *V. corymbosum* in manuals—leads us to the conclusion that it represents nothing more than an enormous collection of interbreeding hybrid segregates which had its origin in the Pleistocene. For the most part, it seems to have been derived from the tetraploids *V. australe*, *V. marianum*, *V. simulatum*, and *V. arkansanum*, which are to be found in reasonably pure form, today, only south of the glacial boundary. This matter has been discussed by Camp (2, p. 201, 202) and by Camp and Gilly (3, p. 347, 348, under the mictonic species); it will be expanded more fully in a later paper.

V. BRITTONII × CORYMBOSUM and V. LAMARCKII × CORYMBOSUM. The tetraploids *V. brittonii* and *V. lamarckii* (both lowbush) are likely to occur in conjunction with the highbush *V. corymbosum* in areas which have been ecologically disturbed. Where they are found together, plants more or less intermediate in stature and possessing all manner of segregate characters are to be found. The halfhigh bushes are so common that they are found in large numbers in certain herbaria. It is primarily by means of these two lowbush entities that the already inherent polymorphy of *V. corymbosum* has been considerably enriched. It is most difficult, if not impossible, to distinguish with certainty between the foregoing tetraploids and the diploid segregates of *V. angustifolium* × *atrococcum* and *V. angustifolium* × *caesariense* on the basis of herbarium material, and quite as difficult in the field where both diploids and tetraploids are present in the same locality.

V. ALTO-MONTANUM × SIMULATUM. As will be noted in a later paper dealing with the taxonomy of the blueberries, *V. alto-montanum* appears to be made up of several biotypes, one of which was described as *V. tallapusae*. Both the high-mountain type (the original *V. alto-montanum*) and the form from lower elevations (*V. tallapusae*) appear to hybridize with *V. simulatum* where their ranges meet.

V. SIMULATUM × ALTO-MONTANUM × LAMARCKII. A series of specimens from near Mountain Lake, Giles County, Va., indicates that *V. lamarckii* is still present this far south. In the same region plants of the apparently tetraploid *V. alto-montanum* may also be found, as well as the known tetraploid *V. simulatum*. While the typical material of all 3 tetraploids for the most part is reasonably ecologically disjunct in the second-growth forest (where sufficiently open) and around meadows and abandoned fields, plants are present that exhibit characters derived from the various paired combinations, with some individuals apparently involving all three species.

V. MYRSINITES × AUSTRALE. Controlled crosses match material found in the wild, the only difference being the greater variability of the wild populations. This is obviously the result of sufficient time in the wild for the production of segregate and back-cross individuals.

"SOUTHERN HYBRID COMPLEX." Five species, all apparently tetraploid, namely, *V. virgatum*, *V. myrsinites*, *V. fuscatum*, *V. australe*, and *V. arkansanum*, are to be found growing together in various combinations in parts of the Coastal Plain region of South Carolina, Georgia, Florida, and Alabama. Where two or more of these come together they form hybrids in all possible combinations, at times yielding local populations which, taxonomically, are almost unsolvable. Unlike the northern tetraploid complex (*V. corymbosum*), which appears not to have produced any hexaploids, the southern tetraploid hybrid complex has been the source of numerous and polymorphic populations of hexaploids, to which the name *V. ashei* is here collectively applied.

Hexaploid Hybrids

V. AMOENUM × ASHEI. There are strong indications that, phyletically, *V. amoenum* is not one of the segments of the *V. ashei* complex, although hexaploid plants derived out of *V. virgatum* × *australe* combinations would be likely to yield segregative extremes superficially similar to it. Instead, it appears to be the culmination of a *V. tenellum* (2x)—*virgatum* (4x)—*amoenum* (6x) autopolyploid series, in which pentaploids also are known from the wild. However, the distribution of *V. amoenum* is such that it touches various segments of the *V. ashei* complex. Where this occurs, hybrids, segregates, and back-crosses are to be found, thus adding to the nomenclatural difficulties of an already perplexing situation.

POSSIBLE REASONS FOR THE ABUNDANCE OF NATURAL HYBRIDS

The question has been raised: "If homoploid blueberries hybridize so easily, why is it that, long ago, they did not become more thoroughly mixed at the different levels of chromosome numbers, resulting in the development of three large amalgamated populations, namely, diploid, tetraploid, and hexaploid?" It must be admitted that there are areas where this would seem to be the easiest solution of our taxonomic problems. But, in answer to that question, we might say that our field studies indicate that conditions for such mixing were by no means common before the advent of the white settlers. Where we have pursued our studies in relatively undisturbed areas, it is indeed rare to find different homoploids occupying the same habitat. That is, there were factors of geo-history and physiology which favored the development and maintenance of geographically and ecologically disjunct homoploids. It has been the disturbance of the ecological balance—the extensive and repeated clearing and burning, the formation of fields and pastures, and often their later abandonment—which made it possible for the various homoploid blueberries to enlarge their ranges and thus make contact, especially since they are a favorite food-source for birds and thus are easily distributed. Because these disturbances favor its dispersal and enlargement of

range, the blueberry population of eastern North America today probably contains enormously more individual plants than it did at the advent of the white settlers; and it is likely that as many interspecific hybrid blueberries have been naturally produced in the last hundred years as in the preceding ten thousand years.[6]

In analyzing the situation, it is our observation that bees are the chief agents of pollination in *Vaccinium*. It has also been noted by many that during the height of the flowering season, individual bees may be selective, visiting only certain species. However, since blueberries flower at the beginning of the vernal period when other nectar-bearing species are at a premium, bees are very likely to be much less particular. We have paid some attention to this item on various occasions and have watched individual bees visit several species of *Vaccinium* in succession; in fact, a scarcity of available flowers only adds to the chance of producing hybrids, for, if two species have somewhat different blooming periods, the latest flowers of one species are likely to be open at the same time as the earliest flowers of the other. Thus the way is opened for the production of interspecific hybrids.

Another item should be noted. We have long observed that isolated colonies of some species are likely to be much less fruitful than those found in the vicinity of another homoploid species. It would seem to follow from this that many individual plants of *Vaccinium* are essentially self-sterile. This, however, is not entirely true; the controlled breeding work so far carried out by ourselves, Morrow (8), and others would seem to indicate the following:

1. While individual plants may be essentially self-sterile, others of the same species may be partially, or even considerably, self-fertile.

2. Those most nearly homozygous are more likely to approach self-sterility than heterozygous individuals.

3. It seems to be usual that individuals even of highly divergent homoploid species are more capable of producing good sets of fruit and more vigorous seedlings when hybridized than when these same individuals are selfed.

In the blueberry there seems to be no interspecific sterility between homoploids. Each species seems to have a basic genom set which is compatible with that in other species. Because self-sterility occurs to a greater or lesser extent in the genus, the development of species seems to have been determined more by geographical and ecological isolation than by genetical isolation.

---

[6] However, we must not forget that certain natural populations (e.g., *V. corymbosum*), which today are widespread, are the result of mass hybridizations during and after the Pleistocene, the result of readjustments along the distributional margins of several homoploids, following large scale climatic and ecological disturbances.

Another item leading to the production of large wild populations of hybrid blueberries is the fact that birds are the primary vectors of the seed. Since the individual fruit commonly contains 10–70 seeds, it is more than likely that the majority of those from a single crossing will be passed at the same time and thus eventually form the nucleus of an interbreeding population. And even if the seed were to be scattered somewhat by subsequent rains or otherwise, it would be that much better, for with competition thus reduced, a larger percentage would be likely to survive; in any event, it is unlikely that the majority would be carried so far that they would not be considered as part of the same potential breeding community. Thus, in spite of the fact that considerable self-sterility exists in *Vaccinium*, the chance of survival and spread of hybrid and segregate populations is notably increased by the manner in which the seed is distributed.

In addition, we must not ignore the fact that the individuals of most species of *Vaccinium* are long-lived perennials. If, for instance, we consider the colony with distinctive leaves alluded to in our opening remarks, and which apparently was not less than a half-mile in diameter, we may roughly calculate its age. This particular clone (belonging to the *V. myrsinites* complex) put out annual underground stolons which seemed to average about a foot in length. If we assume that this clone radiated from its exact center —and that its rate of peripheral growth has been constant—it may be calculated that this plant is not less than 1,000 years old. It may be much older. Nor would this seem to be exceptional, for there is considerable evidence that certain clones of the distantly related box huckleberry (*Gaylussacia brachycera*) have persisted for untold thousands of years, at least since the late Pliocene, or early Pleistocene (1).

Thus, even if an individual did exist which was self-sterile—and near which no other homoploid plants existed—there would be no concern over its immediate fate. If the habitat were congenial, it could persist for at least several milleniums, during which time some adventurous or wind-blown bee might bring a supply of pollen from a homoploid plant, or a passing bird might pause in its branches for a moment and deposit a few seeds of a homoploid plant, thereby setting the stage for another hybrid population. Time and chance must be reckoned with in our considerations.

This longevity of individual clones plays another important role in the production of interspecific hybrids. Following long-term climatic cycles, or more rapidly effective ecological disturbances caused by man's activities, the habitat or ecological association may be so changed in a given area that the general population of one species will be replaced by that of another, better able to persist under the new conditions. However, it is likely that there will always be a few micro-habitats where individual plants of the retreating species will persist long after they have been surrounded by the

advancing species. In line with the foregoing generalities, several specific examples will be mentioned.

There is every evidence that the main body of the population of the diploid *V. angustifolium* has been migrating northward since the last of the Pleistocene glaciations, a movement no doubt accelerated by the post-Pleistocene xeric period. Where once obviously common, it is today known in the highlands south of its present center of abundance in restricted areas, generally in isolated colonies. As the climate shifted and new ecological associates came in, its former sites were taken over by the diploids of the *V. vacillans* complex, better adapted to higher temperatures and dryland conditions. Actually, several of these remaining southern stations of *V. angustifolium* have been located by noting the direction of increase in the proportion of *angustifolium*-like characters in the invading population, the more obvious of which are the decrease in plant and leaf size, and change in leaf shape, coupled with increases in the amount of leaf serration and general "twiggy" condition. In other instances the pure *V. angustifolium* has not been found, but its characters are evident in the plants which have taken over the sites where it must have lingered longest, and where it could have hybridized with the invading plants when they first entered the area.

Other examples are the direct result of man's activities. When observed under undisturbed conditions, the individuals of the northern highbush species are to be found usually in the shrub zone surrounding lakes and open bogs; back of this is a zone of lowland forest with shade so dense as to exclude species of *Vaccinium*. The uplands, having a more open forest type and often with rocky exposures, support populations of various lowbush species. This, therefore, must have been the situation at the advent of the white settlers, for the indigenous Americans, as a general thing, did not carry on an extensive agriculture. Following the clearing of both forest types, the settlers often made attempts to keep these areas open and available for pasture by means of repeated fires. Such conditions exclude the highbush species, but are no bar to the lowbush species because of their underground stolons. Indeed, occasional burning makes these forms more productive. Thus, the lowbush forms, once confined to the uplands, could now successfully migrate into the lowlands sufficiently close to make genetic contact with any homoploid highbush material present. Specific examples which might be cited are the tetraploid combinations of *V. brittonii* and *V. lamarckii* with *V. corymbosum*, and the combinations of the diploids *V. atrococcum* and *V. vacillans*. The same process to a large extent has also been exceedingly active around the pond and slough margins in the southern and southeastern Coastal Plain, other species, of course, being involved.

Since clearing activities produce drier and more sunny habitats, and in the lowlands are often followed by attempts at draining, other effects may

sometimes be noted following the formation of such hybrid communities. In our studies, we have found certain areas where hybrid populations have persisted after the parents have become extinct in the locality. One such instance has been noted in eastern Louisiana where combinations of the highly divergent *V. elliottii* and *V. darrowi* are involved. In fact, such hybrid populations may be particularly suited to some environment and so able to migrate into areas which exclude the parents. For example: certain valleys in Georgia and Alabama, which are pastured and occasionally burned over, have abundant stands of a combination between *V. elliottii* and *V. tenellum*. Here, the rank pasture grass excludes the low-growing *V. tenellum*, and the fire excludes the highbush *V. elliottii;* whereas, the *V. elliottii* × *tenellum* combinations are successful because they are clone-forming and persist by means of underground rhizomes which are not injured by the fire, and yet the plants are sufficiently robust and high-growing to compete with the grass. These populations, in many instances, seem to have migrated down the valleys from the upper reaches and headwaters where *V. tenellum* and *V. elliottii* come together, and where the basic members of the hybrid population were produced. It was probably just such a population migrating down a valley in Georgia that led to a recognition of the material first described as *Cyanococcus cuthbertii* (see the previous discussion of *V. tenellum* × *elliottii* in this paper).

One of the writers of this paper has been observing a highly polymorphic local population of the *V. corymbosum* complex in northeastern Ohio over a period of 25 years—or even longer, if one were to include those times when, as a lad, he ventured into it in quest of berries. During this time the area has been selectively cleared, partly drained, and later intermittently pastured. There was at first a considerable reduction in the total number of plants, and the general aspect of the population has since become markedly changed through natural selection. The remaining segregate biotypes are now becoming effectively established and, barring some new ecological disturbance, seem well on the way toward recapturing most of the available area.[7]

From the foregoing, it may appear that we have placed undue emphasis on our study of natural hybrids. Yet, they are so ever-present that they cannot be ignored, or even dismissed with a brief discussion. Frankly, it was this study of uncontrolled hybrid populations in the wild which opened to us the tremendous possibilities for the horticultural development of the

[7] During one stage of this investigation, a large series of the plants was marked with metal tags, so that particular individuals could be revisited and observed at various seasons and over a period of years. Although the data obtained from the study of this population have never been presented in one place, the numerous and involved questions which arose have had considerable to do with directing the lines into which the present studies of the genus *Vaccinium* have developed.

genus. In fact, in our work we have come upon certain areas which are little else than glorified field laboratories and experimental plots, their populations so diverse that a lifetime of concentrated effort would scarcely begin to duplicate their complexity. In such areas, our work has consisted of the selection of those individuals most likely to be of horticultural value, as well as an attempt to determine the basic species and genetic processes involved. It is scarcely necessary to note that a full understanding of the methods whereby such populations develop is necessary before the taxonomy of the genus can become stabilized.

Furthermore, although we were not aware of it in the beginning, our studies of hybrids have given us the key to a further understanding of the nature and origin of the even more complex allopolyploid populations, so characteristic of the genus. It must have been out of just such hybrid populations that the allopolyploids of the past arose; today, to our certain knowledge, it is where the newer ones are being produced. Taxonomically, these hybrid complexes and allopolyploid complexes are provocative; horticulturally, they are rich in new and worthy combinations.

THE DEVELOPMENT OF NEW HORTICULTURAL MATERIAL

In the development of new and better horticultural material in blueberries, numerous factors are involved. By their very nature, there is not, and probably never will be, such a thing as an all-purpose variety. Let us, for example, consider a single item—the fruit.

Among the fruit qualities to be considered are flavor, size, texture, and color. Yet, having achieved an apparently desirable combination of these characters, other factors must be considered. Are the berries to be used as fresh fruit, are they to be "quick frozen," are they to be incorporated in rapidly-baked pastries, or are they to be canned, and if canned, is their ultimate destiny to be a conserve, a dessert, or an ingredient of pastries? Now this may seem needlessly detailed and considerably involved, but the fact remains that there is a remarkable difference in the reactions of the various kinds of blueberries to the factors of transportation, storage, and the various types of processing and cookery mentioned above.[8] Even the vitamin C content and its stability in storage is known to vary considerably among varieties (6). In general, therefore, the breeder does not attempt the production of an all-purpose berry; instead, a series of special types must be achieved, adequate for the various needs of the trade as well as the home garden.

It should be noted here that the so-called different "brands" of blueberries put on the market by several of the larger Eastern growers' associa-

[8] For example, considerable differences have been noted between various varieties in their reactions to freezing in "consumer packages" (7).

tions refer to no horticultural variety; they represent merely size-classes of the berry. Of course, the growers recognize marked differences in the quality of the varieties under cultivation, but as yet they have made no extensive attempt to educate the buying public. But the day would seem to be not far distant when the careful housewife, the discerning restauranteur, and the progressive packer or canner will demand certain varieties, just as they do of apples, pears, or peaches.

So far as flavor is concerned, in blueberries (as in many fruits) it apparently is the result of a balance between sugars, organic acids, and one or more aromatic compounds, these last generally being present in minute quantities. It is these aromatic compounds that are responsible for the characteristic "blueberry flavor." Some clones produce an overabundance of aromatics; as a result the fruit has a pronounced musky flavor. Fortunately, the aromatics are subject to genetic control and can be built up or attenuated as needed. The same may be said of the sugar and acid content of the various types. In general a so-called "sweet" berry is not necessarily one that has an abundance of sugar but rather one with a relatively low acid content. Of course, climatic factors also affect flavor. It has been noted in many varieties that sunny days and cool nights tend to develop the highest flavor. But, even so, there is a fundamental genetic difference between varieties in their ability to respond to favorable conditions of light and temperature. Flavor, therefore, is within the control of the breeder.

Size of berry is somewhat unpredictable. In general, the higher polyploids of a series have larger fruit than the species with fewer chromosomes. So far, selection and cross-breeding of the larger-fruited sorts seems to have given the best results. Unfortunately for the industry, some of the larger-fruited commercial varieties achieved their prominence largely on the basis of size. For example, the Cabot (fig. 1) was one of the first varieties introduced and in general it has poor dessert quality. From this arose the false supposition that "big berries are not good-flavored." In contrast, Stanley, Pioneer, and other varieties now in cultivation refute this idea. Even the Dixi with berries almost an inch in diameter has better flavor than most wild blueberries. As yet we have no idea what the upper limit of the size of the berry will be (fig. 2). To date, 2 selections have produced fruit in excess of an inch in diameter. However, there might be drawbacks to fruit of such size. In the first place the main axis of the fruit cluster ordinarily is not large enough to support this size of berry, resulting in crowding to the extent that the fruit either is angled, or is forced off the pedicels before the pickers arrive. Since the finding of the Rubel with unusually long internodes on the main axis between the individual pedicels as well as with long pedicels, large-fruited varieties have been bred that do not crowd in the cluster, such as Atlantic, Pemberton, and Jersey. Also, for many purposes a fruit much in excess of an inch in diameter would seem to be undesirable.

FIG. 1. A plant of the Cabot variety about 3 years old. FIG. 2. Right, fruit of the Rubel variety, the best selection yet taken from the wild; left, a large-fruited selection, the result of breeding work. Photographs from the U. S. Department of Agriculture.

Texture has been a rather elusive quality, but is now becoming understood. Several species are known whose fruit with ordinary cooking is unappetizing. They owe this undesirable quality to the presence of large seed and hard placental tissue. However, our field studies indicate that several of the "pulpy" and "seedy" species of berries easily make genetic combinations in which a balance is achieved, the hybrids producing fruit with crisp flesh of high dessert quality. Following this lead, thousands of plants have been produced within the last few years by controlled matings between selected parents of both types. The possibilities of firm-textured berries of good quality, and their advantages to the canning industry and to those growers who must ship long distances are obvious.

The actual color of most fully ripe blueberries is a deep purple-black, but in many species this is masked by a glaucous covering which gives the fruit its characteristic bluish color and is responsible for the common name of the plant. Actually, this covering is an oil-air emulsion which becomes waxy and, as such, is easily lost in handling. Since it is traditional that the blueberry should be "blue" it is of considerable commercial importance that this covering be retained until the fruit is marketed. Unfortunately, some of the better-flavored wild species, and a few of our selections of others, have little or none of this covering and, therefore, are of low commercial value; even berries from cultivated plantations often reach the consumer in poor condition so far as the appearance of the package is concerned. Conversely, we now have available selections from the wild which have a very heavy and durable coating; because of this, they have been called "aluminum berries." These individuals have been found in several species [e.g., *V. myrtilloides* (2x); *V. lamarckii* and *V. alto-montanum* (4x); and *V. constablaei* (6x)].

Another fruit character which should be mentioned is keeping quality. Other things being equal, the deciding factor in the keeping quality of the fruit is the type of scar produced in picking when the berry is separated from the pedicel. If the "brush" (the ends of vascular bundles) separates cleanly leaving a small, smooth, shallow hole with no exudate of sap, the berry ordinarily keeps well; but if some of the epidermis and flesh is torn and removed with the pedicel, organisms of decay soon gain entrance and ruin the fruit. Even if such berries do not decay they shrink badly by drying. Although several of our best-flavored species (tetraploids as well as hexaploids) typically have very bad scars, this may be corrected by selection of plants having fruits with good scars and through controlled crossings with homoploids having nearly perfect scars [e.g., certain selections of *V. lamarckii* (4x), *V. virgatum* (4x), *V. alto-montanum* (4x), and *V. ashei* (6x)].

The length of the period of bud dormancy is important. For example: the commercially most important northern species require a winter dormant

period of at least 800 hours below 45° F, whereas the Gulf Coast species, *V. ashei*, breaks dormancy after less than 250 hours and *V. myrsinites* with a much shorter exposure to this temperature. When such species are used in breeding, care must be taken that the selections for use in particular latitudes have the correct dormant-period requirement, otherwise they may either not break dormancy, or push out too soon and so be injured by late frosts.

From the commercial standpoint, the date of ripening is of great importance. The determining factors are the date of flowering and the length of time required for the ripening of the fruit. Individual clones in the test plots show considerable differences in both these factors; thus, through the use of different horticultural varieties whose habits are known, the grower can markedly extend the season for fresh fruit.

Another characteristic is the length of time over which fruit continues to ripen on the plants. Obviously, it is to the advantage of the commercial grower to have the picking season for a given variety concentrated in a relatively short period, for the reason that production costs are prohibitively increased when the pickers are forced to return repeatedly to the same plants, each time getting only a small portion of the crop. For example, this is one of the faults of the southern "rabbiteye blueberries" (*V. ashei*), in which the picking season is spread over a period of 30 or more days and in some instances of 90 days. Such a length of season is an advantage for the home grower but a disadvantage for the commercial grower. It is considered a serious fault also of the Cabot highbush variety, which has a picking season as long as 40 days. Here two factors are involved; one is the extreme length of the flowering period in the individual inflorescence; and the other is the irregularity in the breaking of dormancy of the inflorescence buds. Careful selection of the better wild clones, together with controlled crossings with other homoploids which do not have this fault, should yield material with considerably improved flowering habits.

Other plant characteristics must also be considered. Here there is a wide range of variables from which to choose; fortunately, plant habit is genetically controlled. From the standpoint of the grower, a plant should produce shoots freely, but not too freely. There should always be on hand a sufficient supply of young, vigorous canes, but they should not be produced in such abundance that the individual plant gets out of hand, interfering both with cultural practices and production. Some of the material is essentially single stemmed and therefore not acceptable for field plantings; other selections tend to sucker excessively and thus produce unwieldy plants. But with these widely contrasting types now available for breeding, it is possible to breed and select varieties of any growth habit desired.

The foregoing has a direct bearing on one of the more important cultural practices in commercial plantings, that of pruning. The majority of high-

bush commercial species each year put forth from the base of the plant several to many new shoots which normally rise to a height predictable for that particular variety. These shoots may grow to full height in one season though usually not until after two or three seasons. These stems or canes may bear when one year old in the case of lowbush species or not until after two or three years in the case of the highbush species. For several successive seasons the plants bear heavily from short (and generally subterminal) branchlets called laterals. After the first year with the lowbush and after several years with the highbush there is a notable decline in the abundance of the crop and the size of the berries, making it advisable to remove the old wood so that a continuous succession of vigorous shoots is available. For this reason lowbush fields are burned over and highbush fields are pruned. Since height is under genetic control and there is available material from 15 inches to 15 feet high, a plant of any desired height between these extremes can be obtained. Lowbush selections with stouter stems and highbush selections of greatest vigor may prove to be the most desirable types.

It has long been supposed by many that commercial blueberries must be grown in areas with sandy soil, a permanently high water table, and with no extreme summer temperature. It may therefore surprise some to learn that, even today, nearly one-half (2,000 to 3,000 acres) of the commercial plantations of highbush blueberries in the United States are of *V. ashei*, and that these are located in Florida (and to a lesser extent in southernmost Alabama and Georgia) generally on upland, often clayey, soils subject to severe drought, where the plants are exposed to high summer temperatures. Nor is there any way to arrive at more than a rough estimate of the size of the crop picked annually from the wild plants of *V. tallapusae* (= *alto-montanum*) and *V. pallidum* in the dry hill-region of Georgia and Alabama. And if one wishes to visit an area which, at times, can be excessively dry and hot, one has only to follow down the Florida peninsula, the natural range of *V. myrsinites*. These are only a few of the species that are not found in wet places and that thrive under conditions of high summer temperatures.

With diploids, tetraploids, and hexaploids available which are not ecologically bound to sandy soils and high water tables, and which are not injured by high summer temperatures, one of the first steps taken in a breeding program is an attempt to enlarge the range of habitat and conditions under which commercial blueberries might be successfully grown. So far, results have been most encouraging.

Like most plants, blueberries are subject to a series of diseases and pests which, under plantation conditions, may become epidemic. While only a beginning toward the production of resistant stock has been made, even a casual examination of any field planting shows marked differences in resistance to the attacks of various pests and diseases, within the same blueberry

species and among the different hybrid combinations. For example, the Black Giant, a variety of *V. ashei*, is fully resistant to stem canker, while adjacent seedlings of the same species have been killed outright by this disease. Such differences suggest the reason that insect and disease resistance is a major part of any breeding program.

In addition to the production of new varieties of blueberries for table use, the group has other potentialities. Among these are its possibilities in soil conservation and wild-life management. Because of the vigorous growth of certain species and their production of extensive colonies by means of interlaced stolons, they may be suited for combating erosion and checking various types of gullying under certain conditions. Furthermore, there is no reason why these same plants should not provide fruit of excellent quality for at least local consumption. Steps already have been taken to provide just such material. It is suggested that certain of these types might also be suitable for use where contour strip and terrace farming are practiced. So far as song birds, game birds, and the smaller animals are concerned, there is scarcely any better cover than a blueberry thicket; nor need we consider only the smaller animals, for every woodsman knows the relation of blueberries to bears; and the plants also furnish excellent browse for deer.

The ornamental possibilities of the group cannot be passed over lightly. Although no particular attempt has been made in our work to develop material especially adapted to ornamental purposes, chance combinations have yielded plants of considerable beauty and grace. There are clones which are unusually large-flowered, some with cascades of pearly white bloom; others are pink, and still others deep red. To those of us who have seen them, the glossy beauty of the *V. australe* × *myrsinites* hybrids is a thing never to be forgotten, And there is scarcely a plant more intriguing than a carefully tended specimen of the dwarf and evergreen *V. myrsinites* as it unfolds its new set of minute leaves and delicate pink flowers. There is now available for further development material that can add gaiety to the spring scene in our gardens because of its splendid trusses of flowers. In midsummer, the deciduous species add a note of stately grace with their arched branches and glossy leaves. And where is there a shrub more striking than *Vaccinium atrococcum* standing in the low sunlight of an autumn afternoon wrapped in its cloak of crimson leaves? Southward, the evergreen plants lend their own peculiar cheer to the winter aspect of gardens and lawns. And the interesting thing is: All of them yield a most delectable crop of food, either for ourselves, or for the feathered guests around our homes. As a group of potential ornamentals, the blueberries have been sadly neglected.

SUMMARY

The blueberries, a floristically and horticulturally important group in eastern North America, are characterized by two outstanding cytogenetic

features: (1) the abundance of polyploids and (2) the rarity of well-marked sterility barriers between homoploids. These two factors, more than any others, have been responsible for the production of morphologically complex populations, and have added to the difficulties of providing an adequate taxonomic treatment along orthodox lines. Conversely, these same factors have been of paramount assistance to those seeking to develop new horticultural material in the group.

The present paper serves to indicate the ease with which hybrids may be produced between individuals of homoploid species under controlled conditions. And the fact that these hybrids, for the most part, are completely fertile further indicates that the majority of the natural populations suspected of being of hybrid and segregate origin have been produced in this manner.

An annotated list of the suspected hybrid combinations observed in the wild is presented. In many instances, these have been duplicated under controlled conditions; in others, the plants thought to be hybrids on purely morphological grounds have been checked and found to be homoploid with species growing in the same region, which species must have furnished the parental material.

The following factors are thought to be responsible for the numerous populations of wild interspecific hybrids present today in the genus: (1) the absence of effective sterility barriers between most homoploids; (2) the presence of a considerable amount of self-sterility; (3) pollination, mostly effected by bees; (4) an early flowering season, when other nectar-bearing species are comparatively scarce; (5) seed distribution, accomplished mostly by birds; (6) the longevity of clones, giving ample time for chance cross-pollination and also (7) permitting individual plants to persist in advantageous micro-habitats in the face of ecological changes; (8) the widespread distributional adjustments of the North American species following the disturbances of the Pleistocene and more recent post-Pleistocene xeric period, permitting them to make ecological contact; (9) the ability of many species to migrate into and become established in areas disturbed by man; and (10) the reluctance of man to destroy a plant which furnishes food and financial remuneration to himself, as well as food and cover for many of his favorite game-birds and wild animals.

Although fields of lowbush blueberries in the northeastern States have been given some special cultural attention for nearly a century, and the highbush varieties have been grown commercially in the United States for about 25 years and notable progress made in the selection and breeding of new forms, the marked horticultural advances of the last few years have been made possible only by an increased knowledge of the cytogenetic and biological situations underlying the group.

The importance of blueberries is pointed out, not only as a source of food, but also as effective agents in erosion control, as wild life cover, and for ornamental effect.

The present paper closes with a survey of the more important factors to be considered in further improvement, together with brief mention of the results achieved up to the present. Important as the recent improvements may seem to be, the writers are convinced that only a beginning has been made.

BUREAU OF PLANT INDUSTRY, UNITED STATES DEPARTMENT
OF AGRICULTURE
BELTSVILLE, MARYLAND
AND
THE NEW YORK BOTANICAL GARDEN
NEW YORK

Literature Cited

1. **Camp, W. H.** 1941. Studies in the Ericales: A review of the North American *Gaylussacieae*; with remarks on the origin and migration of the group. Bull. Torrey Club **68**: 531–551.
2. ———— 1942. On the structure of populations in the genus *Vaccinium*. Brittonia **4**: 189–204.
3. **Camp, W. H. & Gilly, C. L.** 1943. The structure and origin of species. Brittonia **4**: 323–385.
4. **Coville, F. V.** 1927. Blueberry chromosomes. Science **66**: 564–565.
5. **Hedrick, U. P.** 1919. Sturtevant's notes on edible plants. 1–686.
6. **Lineberry, R. A. & Burkhart, L.** 1943. The stability of vitamin C in small fruits. Fruit Prod. Jour. **22**: 164–165, 177.
7. **Moon, H. H., Smart, Helen F. & Caldwell, J. S.** 1936. Varietal suitability of cultivated highbush blueberries for freezing in consumer packages. Fruit Prod. Jour. **15**: 229–231, 248, 251.
8. **Morrow, E. B.** 1943. Some effects of cross-pollination versus self-pollination in the cultivated blueberry. Proc. Am. Soc. Hort. Sci. **42**: 469–472

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 72, NO. 1, PP. 22–30 JANUARY, 1945

DRYOPTERIS, DESCHAMPSIA, PORTULACA, LUPINUS, FAGARA, STENOGYNE, AND DUBAUTIA. HAWAIIAN PLANT STUDIES 12[1]

HAROLD ST. JOHN

POLYPODIACEAE

DRYOPTERIS GOGGILODUS (Schk.) Kuntze emend. Fosberg. In 1942 Fosberg published *D. goggilodus* as a new combination (Bishop Mus., Occ. Pap. **16**: 337–338, 1942). It was based on the original *Aspidium goggilodus* Schkuhr (1809), which had been given an altered spelling when transferred as *Cyclosorus gongylodes* (Schk.) Link (1833). As Fosberg indicates, Link's specific name was an alteration or orthographic variant of the original one by Schkuhr. Subsequent authors generally accepted this altered spelling and placed the species in the generic unit then current. As Fosberg points out, it is now necessary to adopt the original spelling of the specific name, that is *goggilodus*. Though its latinization may be dubious, still the specific name was not an unintentional orthographic error. Hence, the original spelling must be accepted.

The combination *Dryopteris gongylodes* (Schk.) Kuntze (1891) was not an independent new species. It was a transfer based upon *A*[*spidium*] *gongylodes* Schkuhr. Kuntze, thus, accepted Link's altered spelling of the specific name, but clearly made a new combination in *Dryopteris* based upon the original *A. goggilodus* Schk. There were no generally accepted rules of nomenclature during Kuntze's time. He was a zealous reformer and published book after book filled largely with orthographic alterations of the binomials published by earlier botanists. Use of the exact original spelling was to him less important than having a name etymologically correct by his own standards. Hence, he proceeded to "reform" thousands of valid names published by previous botanists. Today we do taxonomic work in conformity with the detailed articles and recommendations of the International Rules of Botanical Nomenclature. Articles 59 and 70 interdict the reformation of botanical names on such grounds as their being badly chosen. Hence, the original spelling must be used, unless it was demonstrably an unintentional orthographic error. Schkuhr's name was not such an error. Fosberg now accepts the original spelling of the specific name, and places it under *Dry-*

[1] This is the twelfth of a series of papers designed to present descriptions, revisions, and records of Hawaiian plants. The preceding papers have been published as Bishop Mus. Occ. Papers **10**(4), 1933; **10**(12), 1934; **11**(14), 1935; **12**(8), 1936; **14**(8), 1938; **15**(1), 1939; **15**(2), 1939; **15**(22), 1940; **15**(28), 1940; and no. 11 is in press. The specimens cited, including the new types, are in the herbarium of the Bishop Museum, Honolulu.

opteris, which seems the correct generic disposition. Earlier, Kuntze made the same combination, except that he used the modified spelling of the specific name, though basing it on the original Schkuhr species. These two names, *Dryopteris gongylodes* (Schk.) Kuntze and *Dryopteris goggilodus* (Schk.) Fosberg are to be considered orthographic variants of the same name. They are comparable to the examples given in the rules under Article 70: *napaulensis, nepalensis, nipalensis,* or *chinensis, sinensis,* or *ceylanica, zeylanica.* Hence, *gongylodes* was not a new name distinct from *goggilodus,* but a mere orthographic variant and there was no need of proposing a new combination under *Dryopteris.* The proper name was available, needing only an etymological alteration back to the original spelling. It now should stand as *Dryopteris goggilodus* (Schkuhr) Kuntze emend. Fosberg.

GRAMINEAE

The native Hawaiian species called by Hillebrand *Deschampsia* were placed by Skottsberg in the genus *Aira.* For several decades there was a taxonomic and nomenclatorial confusion between these two genera and *Aspris.* Now this has been settled by the selection of *Aira praecox* L. as the lectotype of the genus *Aira* (Internat. Rules Bot. Nomencl. ed. 3. 139. 1935). This generic name is thus stabilized for the species without prolongation of the rhachilla and with the lemmas terminating in two slender teeth. Then, there is no need of the generic name *Aspris* which becomes a synonym of *Aira. Deschampsia* when first described contained many species now considered of several genera. When the various generic segregates were removed, the plurality of species were representative of *Deschampsia* as traditionally accepted for the species with the rhachilla prolonged behind the upper floret, and the lemmas truncate, erose-dentate at summit. Hitchcock in his Grasses of Hawaii (Mem. Bishop Mus. **8**(3): 143–145. 1922), when following the American Rules, placed the native Hawaiian species in *Aira.* Now, under the International Rules, these species with prolonged rhachilla and truncate lemmas should be placed in *Deschampsia.*

Deschampsia hawaiiensis (Skottsb.) St. John, comb. nov. *Aira hawaiiensis* (Hillebrand herb.) Skottsb. Medd. Göteborgs Bot. Trädgård **2**: 205–207. *f. 1b, c.* 1926. *D. australis* Hillebrand, Fl. Haw. Is. 520–521. 1888; not Raoul, 1846.

DESCHAMPSIA HAWAIIENSIS (Skottsb.) St. John, f. **depauperata** (Skottsb.) St. John, comb. nov. *Aira hawaiiensis* (Hillebrand herb.) Skottsb. f. *depauperata* Skottsb. Medd. Göteborgs Bot. Trädgård **2**: 207–208. 1926.

DESCHAMPSIA HAWAIIENSIS (Skottsb.) St. John f. **haleakalensis** (Skottsb.) St. John, comb. nov. *Aira hawaiiensis* (Hillebrand herb.) Skottsb. f. *haleakalensis* Skottsb. Medd. Göteborgs Bot. Trädgård **2**: 207. 1926.

PORTULACACEAE

PORTULACA CYANOSPERMA Egler, Bishop Mus. Occ. Pap. **18**(15): 167–170. 1937.

OAHU: Waianae, dried alluvial flat, north of Mauna Kuwale, alt. 300 ft., Nov. 11, 1941, Mrs. Juliette Oliviera Wentworth.

The specimens were transplanted and cultivated in Honolulu. They were grown in pots at the Pineapple Research Institute. Those placed outdoors in the sun became depressed but with many vigorous branches; the crowded leaves 7–21 mm. long, 1–4 mm. wide, flattened, linear to narrowly oblance-linear, and mostly strongly tinged with red; and the flowers abundant. Those grown in the greenhouse were more or less erect, of loose growth; the remote leaves 12–33 mm. long, 1–3 mm. wide, flattened, linear; and the flowers few. The flowers open about 10 a.m. and close in the early afternoon. Herbarium specimens were made from these July 31, 1942. They differ from the characters given by Dr. Frank E. Egler only in having the hairs subtending the flowers only 5–7 mm. long instead of 1 cm. long. This is not deemed of importance, especially as Egler himself demonstrates the variability in length of the hairs in the leaf axils, averaging about 5 mm. in length.

The color of the petals was Phlox Purple (Ridgway, R., Color Standards and Color Nomenclature pl. 11, 1912) or (Maerz, A. & Paul, M. R., Dictionary of Color pl. 52, 12E, 1930).

The species was previously known only from the islands of Lehua and Kauai. Hence, this Oahu locality is an interesting range extension. The potted plants seed prolifically and scatter their seeds around. They have seeded in this way the vicinity of the spots where they have been cultivated in Honolulu. Mrs. Wentworth assures the writer that there is no possibility that the plants growing naturally in the arid western part of Oahu at Waianae could have in any way sprung from the Lehua plants cultivated on the opposite side of the island in Honolulu by Caum and Egler.

LEGUMINOSAE

LUPINUS ALBUS L. var. TERMIS (Forsk.) Alefeld. "Lupine," "Tremoço" (Portuguese).

MAUI: Haiku Uka, Olinda, 3,800 ft. alt., cult., Aug. 4, 1943, *H. St. John 20,359*.

The plant is vigorous, from 1–1.8 meters tall, with blue flowers and abundant, large pinkish seeds. The seeds after leaching for a week are cooked and eaten by the Portuguese.

RUTACEAE

FAGARA DIPETALA (Mann) Engler var. **geminicarpa** (Rock) St. John, comb. nov. *Xanthoxylum dipetalum* Mann. var. *geminicarpum* Rock, Ind. Trees Haw. Is. 209–210. *pl. 81–83*. 1913.

FAGARA MAUIENSIS (Mann) Engler var. **anceps** (Rock) St. John, comb. nov., f. **petiolulata** (Rock) St. John, comb. nov. *Xanthoxylum mauiense* Mann var. *anceps* Rock f. *petiolulatum* Rock, Ind. Trees Haw. Is. 205–206. 1913.

LABIATAE

Stenogyne mollis (Sherff) St. John, comb. nov. *S. rugosa* Benth. var. *mollis* Sherff, Bot. Gaz. **96**: 141–142. 1934.

This was published as a variety and briefly diagnosed by Sherff in 1934; later in his monograph (Bishop Mus. Bull. **136**: 67–68. 1935) he cited numerous collections of it. It is a characteristic plant of the western slope of the island of Hawaii, occurring at Waikii on the side of Mauna Kea, on Hualalai, and abundantly in Kona.

It differs markedly from *S. rugosa* in its abundant uniform pubescence; in the calyx lobes all shorter than the tube and oblong or oblong-lanceolate and merely acute, not subulate, tipped; and in the corolla shorter, only 12–15 mm. long. *S. rugosa* is sparsely hirsute to glabrate; the calyx sparsely hirsute or glabrous; the calyx lobes lanceolate, acute and subulate tipped; and the corolla 14–22 mm. long. This latter species occurs on both east and west sides of the island of Hawaii. Since the var. *mollis* has numerous and constant characters that seem to be adequate and diagnostic, and as it has a different range, it is here raised to specific status.

STENOGYNE RUGOSA Benth. *S. rugosa* Benth. var. *subulata* Sherff, Bot. Gaz. **96**: 142. 1934; Bishop Mus. Bull. **136**: 68. *f. 22.* 1935. *S. kaalae* Wawra var. *coriacea* Degener & Sherff ex Degener, Fl. Hawai. fam. 316. 13 S 1935.

Stenogyne kaalae var. *coriacea* is maintained by Sherff in his monograph of the genus (Bishop Mus. Bull. **136**: 76, 1935). Cotype material and more recent collections from Kilauea, Hawaii, *Fagerlund & Mitchell 3,* and *15,* can easily be run through Sherff's key to var. *coriacea.* This was keyed on the purely numerical basis of whorls 2-flowered, versus whorls 6- (or 2–4–8–10) flowered. Comparison shows that var. *coriacea* of the island of Hawaii differs from *S. kaalae* of the Waianae Mts., Oahu, in aspect and in leaf shape, toothing, short pubescence, calyx and corolla pubescence. It does not seem most closely related to that species. Further comparison shows it to be identical with *S. rugosa* var. *subulata* of the island of Hawaii. Single branches of var. *coriacea* have the whorls 2-, 4-, or 6-flowered, and this was well shown in the original illustration in Degener's Flora Hawaiiensis. The var. *coriacea,* since it agrees in structure, is not separable from *S. rugosa* var. *subulata.*

A reexamination of *S. rugosa* and its var. *subulata,* using specimens cited by Sherff, reveals a different status of the diagnostic characters, as follows: *S. rugosa* has the petioles 3–22 mm. long; blades 1.7–9.3 cm. long, 1–4 cm. wide, from narrowly oblong-lanceolate to lanceolate and ovate, acute; calyx

lobes subequal to the tube, lanceolate, acute or subulate tipped. The var. *subulata* has the petioles 5–17 mm. long; blades 2–7 cm. long, 0.8–2.8 cm. wide, from narrowly oblong-lanceolate to lanceolate and ovate, acute; calyx lobes subequal to the tube, lanceolate, acute or subulate tipped.

The leaves are of various shapes, but several such are to be found on a short section of a stem. The larger and broader leaves are usually on the main or ascending branches, while the narrower blades occur on smaller lateral branches or more often on prostrate, weak branchlets. The calyx is accrescent from bud to fruit, increasing materially in size. Its orifice is markedly oblique, with the upper tooth much shorter than the lateral or especially the lower ones. A contrast made between the length of calyx tube and calyx teeth without qualification as to which teeth were examined is of little value. Actually the upper tooth is much shorter than the tube, the lateral teeth are subequal to it, and the lower teeth exceed it in length. There are no discernible differences in pubescence of petiole. The leaves show the same gamut of shapes in both. The calyx shape and toothing is identical. From the expanded measurements given here, it will be seen that some individuals of *S. rugosa* have somewhat longer petioles, longer and wider blades, but the measurements largely overlap and the fact that some specimens of the species are slightly larger in size of their largest blades may be correlated with the fact that the specimens of it are more numerous than those of the variety. This new study of the specimens and reevaluation of the characters indicates clearly that the variety *subulata* Sherff has no diagnostic differences, so it is here placed in the synonomy of *S. rugosa* Benth.

COMPOSITAE

DUBAUTIA PLANTAGINEA Gaud. var. **typica** St. John, var. nov. *D. plantaginea* Gaud. Voy. Uranie Bot. 468. 1830; Atlas *pl. 84*. 1830. *D. plantaginea* Gaud. var. *Chamissonis* Sherff, Am. Jour. Bot. **20**: 616. 1933; Bishop Mus. Bull. **135**: 86–87. *f. 29*. 1935. *D. plantaginea* Gaud. var. *angustifolia* Sherff, Am. Jour. Bot. **20**: 616. 1933; Bishop Mus. Bull. **135**: 187–188. 1935.

Sherff pointed out that Gaudichaud's illustration of *D. plantaginea* showed a panicle with markedly alternate branches. This character was also mentioned in Gaudichaud's brief description. Sherff matched the illustration with two collections from the island of Lanai and removed all specimens from Oahu from the species proper, thus differing from the interpretations of previous botanists. He described the Oahu specimens as var. *Chamissonis* Sherff which was said to differ by having the "Principal branches of the panicle opposite."

For some time the writer has intended to check over this group, for it is well known that the Urania Voyage did not visit Lanai, so Gaudichaud could not have collected a species restricted to the mountains of that island.

The only subsequent collections from Lanai, accepted by Sherff as *D. plantaginea,* are in the Bishop Museum and are at hand. *Munro 48,* Dec. 23, 1913, Lanaihale, has one flowering branch. Its stem is swollen and blighted at apex, is clearly diseased, and perhaps injured by a borer. From the uppermost axils it bears four slender, spindly branches. One is vegetative but produces only shortened, lanceolate, bract-like leaves. The other three are flowering, one with buds, the other two with flowers and fruit. The panicles are reduced, 8–12 cm. long, 5–7.5 cm. wide, and the lower and principal branches are alternate. On the sheet is another stem, also blighted at tip, but its axillary branchlet is vegetative with normal, linear-oblanceolate leaves 11–12 cm. long, 18–22 mm. wide.

The remaining modern collection is also from Lanai, Waiopaa, *G. C. Munro 271.* Its flowering specimen is also on a stem swollen and blighted at the apex. Just below this blighted apex, spring two axillary branchlets, slender, but fairly well developed, and bearing fruiting panicles 7.5–8 cm. long, 4–6 cm. wide, the principal branches of which are alternate or subopposite. Thus it is found that the only two modern collections accepted by Sherff as matching exactly Gaudichaud's type from the Uranie Voyage are two specimens with injured main stems, and reduced panicles produced on the weak secondary branchlets. Gaudichaud's illustrations are often more revealing of details than the brief Latin diagnoses. For years I have used his book and I have compared it with the types in Paris, and with fresh, living specimens in the Hawaiian Islands. The steel engravings are striking, bold, and attractive, but in fine detail, particularly of pubescence, they are often inaccurate. On gross detail they are excellent. There is no explanatory statement, but I have concluded that nearly all the habit drawings were made life size. The inflorescence of *D. plantaginea* is shown as 16 cm. long and 10.5 cm. wide. This agrees well with the sizes of normal plants on Oahu or Lanai, but not with the ones from weak secondary branchlets, as in the two cited by Sherff as typical. He gave the measurement as "± 1 dm. long." Hence, the size of the inflorescence cannot be used as a sound diagnostic character.

Sherff gives the ranges as *D. plantaginea* from Lanai; while the var. *Chamissonis* as from Kauai, Oahu, Maui, and Hawaii. He must have made an oversight, for in his revision, p. 87, under Specimens examined, he cites three collections from the island of Lanai: *Forbes 284.L; Forbes 299.L;* and *Munro,* Nov. 11, 1916. One is vegetative, but the others are in bud or flower. In the most mature one, *Munro,* Nov. 11, 1916, the panicle is 15 cm. long, 20 cm. wide. In stem, leaf, and inflorescence, it is a good match for the Oahu plants. The branches of the inflorescence are opposite. There is another, more recent, Lanai fruiting specimen now at hand, Kaiholena Gulch, *F. R. Fosberg 12,505.* Its inflorescence is 15 cm. long and about 12 cm. wide.

The collections of var. *Chamissonis* have been studied to test the constancy of opposite branching of the inflorescence. The great majority have the inflorescence with the lower and median branches opposite, but towards the tip there is a change to subopposite or commonly to alternate. With this as the mean, it is not surprising to find exceptions. The following collections from Oahu, and all but the first and last cited by Sherff, have the lower one to three nodes producing alternate branches. These are, from the Waianae Mts.: Puu Kaala, *St. John 9,925;* Puu Kaala, *Fosberg 10,363;* Mt. Kaala, Nov. 13, 1929, Y. Tanaka; Puu Kaua, *Fosberg 9,007;* from the Koolau Range: Pauoa, *Garber 140;* and Kipapa Gulch, *Hosaka 1,242.* It is concluded that alternate branching of the inflorescence is occasional, especially on weak secondary branchlets. In any case, it is not constant, and it does not appear significant.

The only remaining differences mentioned by Sherff are: *D. plantaginea* having the leaves "at base more or less widened and clasping the stem"; var. *Chamissonis* having the leaves "more or less narrowed toward base and semi-amplexicaulous." This sounds like the recognition of a broad leaved and a narrow leaved variant. Close study of the many cited specimens and of others shows no difference whatever. The qualifying phrase "more or less" seems to make the words widened and narrowed, quite meaningless, as used by Sherff.

The geographic range of var. *Chamissonis* Sherff was carelessly handled by Sherff. His half page of Specimens examined, lists many from Oahu and three from Lanai. His summary of range is:

"Distribution: islands of Kauai, Oahu, Maui, and Hawaii." He failed to include Lanai, instead adding to Oahu the islands of Kauai, Maui, and Hawaii for which no collections were cited, nor are any now known to the writer. Sherff's method of citing collections alphabetically under the collectors may be convenient for him, but it obscures all geographic correlations and gives the user the very tedious task of scanning every line if he seeks information on where the plant grows. Then, if Sherff's summary of distribution is wrong, as in this case, it may go undetected for years.

In summary, the characters given for var. *Chamissonis* Sherff are either nonexistent or lacking in significance. Gaudichaud could not have collected the type of *D. plantaginea* on Lanai because he did not visit that island. The Lanai plants prove to be inseparable from the Oahu ones. Hence, var. *Chamissonis* is reduced to the synonomy of *D. plantaginea* Gaud.

Dubautia plantaginea Gaud. var. *angustifolia* Sherff was described in 1933 and given a 1½-line diagnosis and a type citation. In 1935 Sherff in his subsequent revision gave a 2-line description in English, an exact translation of the Latin diagnosis except for the added words: Leaves narrowed below, more elongate. Besides the type he cited eleven other collections. Eight of

these are before me. The key characters agree with the details given in the description:

a. Principal leaves 1–2 dm long and commonly 1–3.4 cm wide - - - -
a. Principal leaves about 1.2–1.9 dm long and 0.7–1.3 (rarely –1.6 cm wide - - - - - - - - - - variety γ angustifolia

Neither a first nor a repeated reading of those lines will reveal any tangible key characters. A key should single out the diagnostic differences, but this one fails to do so. The making of keys is an art, well mastered by some botanists, but not by others. The excellence of the key is a good test of the finished quality of taxonomic work. There are numerous similar stumbling blocks in the keys in the now numerous, hurried revisions of Hawaiian genera by Sherff. These treatments and keys have proven to be the despair of students of the Hawaiian flora.

These critical remarks do not dispose of var. *angustifolia* Sherff. The name is valid and it was effectively published. Even though its key character is worthless, it still might have distinctive characters and be a good variety. It is recorded on Oahu from Mt. Kaala in the Waianae Mts.; and in the Koolau Range from the Waikane-Schofield trail to Puu Konahuanui. The closest relative, as treated by Sherff, is the var. *Chamissonis* Sherff which also occurs in the same zone at every one of the recorded localities. Hence, var. *angustifolia* has no distinct geographic range. The latter variety was stated to have more elongate bracts of the inflorescence. Comparison with the very numerous specimens of var. *Chamissonis* reveals that this is not so, and not even a tendency towards longer bracts is detectable. There remains only the alleged leaf character, its size and particularly its width. The type specimen of var. *angustifolia* from Nuuanu, Oahu, Sept. 1860, Hillebrand (Kew) has not been available, but a satisfactory judgement seems possible from the eight paratypes at hand. The specimens of var. *Chamissonis* labeled and cited by Sherff show some with narrow, some with intermediate, some with broader principal leaves. The minimum width is 1 cm. and the maximum 3.4 cm. Between these extremes are all gradations. Some of those with the narrowest leaves were separated as var. *angustifolia*, but not all. The two following, studied and cited by Sherff as var. *Chamissonis* have all the appearance of and are inseparable from his var. *angustifolia*. These are, Oahu: Pauoa, *Rock 1055;* and Waiolani, *Forbes 1848.0*. As in any species population there are extremes between which the leaves of individuals show fluctuation. This is so here. There is a range of fluctuation from narrow to broad extremes. There is no perceptible break in the series. Regardless of the inadequacy of Sherff's key, the narrower leaved plants are not separable on having leaves less than 1.9 cm. wide or at any other figure. There is such a complete fluctuation in leaf width; there are no other known characters; there is no geographic separation; so that it is clear to the writer that var. *angustifolia* must be

merged with var. *Chamissonis* which as demonstrated itself becomes a synonym of *D. plantaginea* Gaud.

For a species with numerous varieties, it is helpful to have the original sort given a name, such as var. *typica*.

DUBAUTIA PLANTAGINEA Gaud. var. STRIGOSA Skottsb. Medd. Göteborg Bot. Trädgård **2**: 277. 1926; sensu Sherff, Bishop Mus. Bull. **135**: 88. 1935, as to specimens from the island of Hawaii, not as to those from Maui and Oahu.

Leaves below appressed pilose; involucral bracts 5–5.5 mm. long, the back short capitate glandular and towards the tip sparsely hirsutulous, the margin sparsely hirsutulous ciliate towards the tip.

TYPE: island of Hawaii, Kohala Mts. above Kamuela (Waimea), 1,100 m., Sept. 29, 1922, *C. Skottsberg 733* (Ho.).

Specimens examined: all from Hawaii, Kohala, *W. Hillebrand & J. M. Lydgate;* Kohala Mts., Waimea, Sept. 7, 1911, *C. N. Forbes 490.H;* Hualalai, Puuli crater, 5,000 ft., June 11, 1909, *J. F. Rock 3,679 (217)*.

The two following varieties are described on material included by Sherff in his concept of var. *strigosa* Skottsb.

DUBAUTIA PLANTAGINEA Gaud. var. **pauoaensis** St. John, var. nov.

Foliis infra adpressi-pilosulis, bracteis involucri 4–4.5 mm. longis dorso sparse puberulenti deinde subglabrato marginibus puberulo-ciliatis apicem versus.

TYPE: Oahu, Pauoa Valley, Jan. 8, 1910, *J. F. Rock 215* (Ho.).

DUBAUTIA PLANTAGINEA Gaud. var. **glandulosa** St. John, var. nov.

Foliis infra adpressi-villosis, bracteis involucri 3.8–4.3 mm. longis, ad basim capitato-glandulosis et remote hirsutis, dorso glabro, marginibus dense pilosuli-ciliatis.

TYPE: Eastern Maui, Kahikinui, Oct., 1910, *J. F. Rock 8,652* (Ho.).

Specimens examined: all from Maui, South Haleakala, Ex Museo botanico Berolinensi, presumably by W. Hillebrand; south slope of Haleakala, east of Puu Pani [= Puu Pane], sterile tree, 12 ft. high, March [= April] 4, 1920, *C. N. Forbes 2,135.M.*

UNIVERSITY OF HAWAII

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 72, NO. 1, PP. 31–41 JANUARY, 1945

THE JATROPHAS OF CERVANTES AND OF THE SESSÉ & MOCIÑO HERBARIUM

ROGERS MCVAUGH

Among the several hundred species names published in the genus *Jatropha*, of the Euphorbiaceae, are 8 published in 1794, with brief descriptions, by Vicente de Cervantes, who at that time held the chair of Botany in the Royal Botanical Garden in Mexico City. All these names relate to Mexican species, but are so briefly characterized as to make their identification all but impossible from the descriptions alone, and none of them is currently applied to any known species of *Jatropha*. It is now possible, however, to associate most of Cervantes' names with definite species, on the basis of contemporaneously named specimens from the herbarium of Sessé & Mociño, now on deposit at the Field Museum.

To Mr. Paul C. Standley of the Chicago Natural History Museum (Field Museum), who read this paper in manuscript, I am very grateful for his assistance in locating and assembling the numerous specimens involved, for his suggestion that some of the supposed species of *Jatropha* were in reality species of *Manihot*, and for his kindness in supplying some of the historical details in reference to the collection of Sessé and Mociño.

Cervantes, who was a member of the Botanical Expedition headed by Sessé which was sent to New Spain by Charles III, was Professor ("Catedrático") in the Royal Botanical Garden from 1788 until 1820 and perhaps until his death in 1829.[1] The most detailed account in English of his work and that of the other members of the Expedition to Mexico is that by Standley (Contr. U. S. Nat. Herb. **23**: 13–18. 1920). He seems to have devoted most of his time to his professorial duties, for although he was rather well known to European botanists through correspondence, his published works were few. He was the author of a few short papers in the Anales de Ciencias Naturales, and his comprehensive account of the Central American rubber tree was published as a 35-page supplement to La Gazeta de Literatura [volume 3], on July 2, 1794, with the title: "Discurso pronunciado en el Real Jardin Botánico el 2 de Junio por el Catedrático Don Vicente de Cervantes"; this paper was translated into English and published in abridged form in 1805, in König's *Tracts Relative to Botany* under the title of "Account of the Ule-tree (Castilla elastica), and of other trees producing the

[1] Dr. H. W. Rickett supplies information that records of the Botanical Garden in the National Archives of Mexico cease with the year 1820.

elastic gum." The "other trees producing the elastic gum" included several Jatrophas, of which Cervantes (1794, p. 3) wrote:

"En las tierras calientes de este Reyno abundan muchas especies del mismo género Yatropha, como son la *mala Muger*, (3) el árbol *de los Piñones de Indias* (4) y otras varias especies conocidas (5) y nuevas (6) descritas por el citado Señor Director [i.e. Sessé, to whom Cervantes has just referred as Don Martin de Sesé y Lacasta] en la Flora Mexicana.

"(3) Jatropha urens.

"(4) J. Curcas

"(5) Manihot. Jan J. Janipha. J. Herbacea Linn.

"(6) [Here follow the descriptions of the 8 newly proposed species]."

From the above it seems clear, as Sprague (Kew Bull. **1926**: 418. 1926) has already suggested, that the descriptions published by Cervantes were taken directly from the projected but unpublished *Flora Mexicana* of Sessé and Mociño; additional evidence for this may be found in the descriptions themselves, all of which end with a citation of "Flor. Mex." or "Flor. Mex. cum icone."

Most of the specimens in the herbarium of Sessé and Mociño were identified by them, at least to the genus; where possible, they identified their plants with Linnean species or those of the few other authors available to them. When they deemed this impossible, their specimens were designated by manuscript names which were intended for publication in the *Flora Mexicana*, these names often being accompanied by "N." [for "Nobis"] or "ic." [referring to one of the plates for the flora]. The Jatrophas (including *Cnidoscolus*) in their collection are similarly labelled and are listed below, arranged according to the arbitrary numbers assigned the specimens at Madrid:

Number	*Identity of Specimen*	*Notation by Sessé & Mociño*
4220	*Jatropha gossypifolia* var. *elegans* (Pohl) Muell. Arg.	"Jatropha gossypifolia."
4221	*Jatropha cathartica* Ter. & Berl. [*J. Berlandieri* Torr.].	"Jatropha[2] . . . N. Communicavit et misit D. Ignatius Leon."
4223	*Jatropha multifida* L.	"Jatropha multifida. ic."
4225	*Cnidoscolus Chayamansa* McVaugh.	"Jatropha urens."
4226	*Jatropha olivacea* Muell. Arg.	"Jatropha ciliata N. Jatropha foliis lobatis ciliato-glandulosis."
4227	*Cnidoscolus tubulosus* (Muell. Arg.) Johnst. [*Jatropha tubulosa* var. *septemloba* Muell. Arg.].	"Jatropha quinqueloba N. Jatropha foliis palmatis 5-lobis dentatis inermibus basi biglandulosis."
4228	*Manihot foetida* (H.B.K.) Pohl.	"Jatropha triloba N. Jatropha foliis trilobis integerrimis."
4229	*Manihot foetida* (H.B.K.) Pohl.	"Jatropha[3] . . . N. peltata."
4230	*Manihot* sp.	"Jatropha palmata N. Jatropha foliis palmatis lobis obtusis integerrimis."
		"Arbuscula 15 ped. Flores nudi."
4231	*Jatropha podagrica* Hook. and ?*Jatropha platyphylla* Muell. Arg.	"Jatropha peltata N. ic."

[2] Specific name never published in this genus.

[3] Unpublished specific name crossed out "peltata" substituted.

Number	*Identity of Specimen*	*Notation by Sessé & Mociño*
4232	*Cnidoscolus angustidens* Torr.	"Jatropha herbacea. Jatropha aculeata foliis trilobis dentato-sinuatis, caule herbaceo. Radix tuberosa lactescens. Caul. sesquiped."
4233	*Jatropha Curcas* L.	"Jatropha edulis N. ie."
4234	*Jatropha* sp., near *J. Alamani* (leaf only).	"Jatropha cureas."
4235	*Jatropha* sp., near *J. Alamani*.	"Jatropha."
4236	*Jatropha* sp., near *J. Alamani* (leaves only).	"Jatropha cureas."
4237	*Jatropha Alamani* Muell. Arg.	"Jatropha cureas."
4238	*Jatropha spathulata* var. *sessiliflora* (Hook.) Muell. Arg.	"Jatropha dioica N. ie. Vgo. Sangre de drago."
4243	*Jatropha hastata* Jacq. [*J. integerrima* Jacq.].	"Jatropha molucensis. Havan. Peregrina."
4244	*Jatropha cinerea* (Orteg.) Muell. Arg., and *Jatropha cordata* (Orteg.) Muell. Arg.[4]	"Jatropha moluecana."
4245	*Jatropha cordata* (Orteg.) Muell. Arg.	"Jatropha[2] . . . N."
4246	*Jatropha hastata* Jacq. [*J. integerrima* Jacq.].	"Jatropha molucana ie."
4247	*Jatropha hernandiaefolia* Vent. and *J. hastata* Jacq.[5]	"Jatropha heterophylla N."

It will be seen that the authors of the comments and notes quoted above used six Linnean names, evidently with full knowledge of their origin; in addition to these, their herbarium contained ten species which they considered new to science, and for which they intended to propose new names. One of these (*Jatropha heterophylla*) was published in the *Flora Mexicana* (ed. 2. 224. 1894); two of them seem never to have been published; the remaining seven were published, not in the ill-fated volumes which appeared under the names of Sessé and Mociño late in the 19th century, but by Cervantes in 1794! Cervantes' descriptions, although brief and unsatisfactory, are sufficiently diagnostic to make it clear that they apply to the species in question, those labelled with his names in the herbarium of Sessé and Mociño.

Parenthetically it may be pointed out, with reference to the above table, that the name *Jatropha moluensis* (Fl. Mex. ed. 2. 224. 1894) was probably never intended for publication, being evidently a misprint for *molucensis* (see no. 4243 above), which in its turn seems to have been carelessly used in place of *moluccana*, the Linnean name which the authors understood to apply to the plant we know as *Jatropha hastata* Jacq. Since the name *moluensis* was published, however, this specimen may be taken as the type.

[4] A single leaf of *J. cordata*, quite possibly derived from no. 4245.

[5] A portion of an inflorescence of *J. hastata*, quite possibly derived from no. 4246. *J. heterophylla* is to be typified by the other element.

With this corroboration from herbarium specimens, we are probably justified in supposing that the Sessé and Mociño plants are to be regarded as the types of Cervantes' species, since there are no apparent discrepancies between the specimens themselves and the published account, either in names or in descriptions. It is necessary to make the reservation that in the Sessé and Mociño herbarium as it has come down to us there are some known additions and mixtures and misplaced data, so that we are not always able to associate names and specimens with entire confidence; in these particular cases, however, our assumptions appear to be justified.

Since Cervantes definitely named Sessé as the author of the descriptions, the species are to be attributed to him rather than to Cervantes. A formal discussion of the 8 species follows:

1. JATROPHA PELTATA Sessé apud Cerv. Gaz. Lit. Mex. **3**: supl. 3. 1794; König, Tracts Bot. 231. 1805. The original description reads: "Jatropha (Peltata) floribus caliculatis, folijs peltatis. Flor. Mex. cum icone." This plant, if actually a *Jatropha* and a Mexican or Central American species, can be nothing except *J. podagrica* Hook. or *J. platyphylla* Muell. Arg. Among the Sessé and Mociño plants are two collections labelled *Jatropha peltata;* the first of these, no. 4229, seems to have been referred to this species as an afterthought, the authors having previously crossed out the name of another proposed species; the plant is *Manihot foetida*, which does not have peltate leaves; the second collection named *Jatropha peltata* (no. 4231) consists of (1) a fragment of an inflorescence which can be definitely identified as that of *J. podagrica*, since it has the short glabrous calyx and blunt rounded entire discrete lobes of that species, and (2) the major portion of a small and perhaps immature leaf which cannot be identified with certainty but is probably that of *J. platyphylla;* this is indicated by the rather prominent venation and the marginal pubescence characteristic of this species and not of *J. podagrica*, which normally has thick and entirely glabrous blades with slender and rather inconspicuous veins. Sessé and Mociño are known to have collected *J. platyphylla;* a considerable specimen is in the Delessert Herbarium, and is represented in the Field Museum by fragments of leaf and inflorescence and by Field Mus. neg. 24389. If *Jatropha podagrica* was collected by some member of the botanical Expedition, it may well have been in Guatemala, where this species is often cultivated; but if so the above specimen could hardly be the type of *Jatropha peltata* Sessé, for Mociño, the first member of the Expedition to reach Guatemala, did not arrive there until about December 1, 1796, two and one-half years after the publication of *J. peltata*. For this fact I am indebted to Dr. H. W. Rickett.

It would be most unwise to take up the name *Jatropha peltata* for either of the species now well known under other names, in view of the mixture of species included under this name in the Sessé and Mociño collection,

especially since it is probable, but not proven, that the specimen of *Jatropha podagrica* was added to the collection after 1794. It should be noted, however, that *Jatropha peltata* Sessé has priority over *J. peltata* H.B.K. (Nov. Gen. & Sp. 2: 83. 1817), which may therefore be called **Jatropha Humboldtiana** McVaugh, nom. nov.

2. JATROPHA EDULIS Sessé apud Cerv. l.c.; König, l.c. The original description reads: "Jatropha (edulis) floribus caliculatis, folijs cordatis integerrimis sublobatisque. Flor. Mex. cum icone." This is clearly the nearly entire-leaved form of *Jatropha Curcas* represented by the Sessé & Mociño specimen (no. 4233). The leaves are almost conventionally cordate and practically unlobed, not at all like the usual form in this species. Essentially the same form was described as *Jatropha yucatanensis* Briq. (Ann. Conserv. Jard. Bot. Génèv. **4**: 230. 1900); the type, collected at Campeche by Linden in 1840, is in the Delessert Herbarium and is represented in the Field Museum by fragments of leaf and inflorescence and by Field Mus. neg. 24393.

3. JATROPHA CILIATA Sessé apud Cerv. Gaz. Lit. Mex. **3**: supl. 4. 1794; König, l.c.; *J. olivacea* Muell. Arg. Linnaea **34**: 207. 1865; *J. grandifrons* I. M. Johnst. Contr. Gray. Herb. **68**: 89. 1923. The original description reads: "Jatropha (ciliata) floribus caliculatis: foliis cordatis ovatis ciliato denticulatis. Flor. Mex. cum icone." From the description this could hardly be any Mexican species except *J. Alamani* Muell. Arg., *J. olivacea* Muell. Arg., or *J. cordata* (Orteg.) Muell. Arg. Both the first and the last appear to have been known to Sessé and Mociño and presumably to Cervantes under the other names, and the ample flowering and foliage specimens under this name in the herbarium (no. 4226) are unquestionably *J. olivacea*. This species was known to Mueller only through a collection (not seen by me) made by Liebmann at San Juan del Estado, Oaxaca; it has since been recollected at the type-locality (*L. C. Smith 467*, May 6, 1895), and is known from various localities in central Oaxaca and from Río de San Francisco, Puebla (*Purpus 4050*, August 1909) and from the Valley of Mexico (Hill of Ixtapalapa, *Pringle 6348*, June 13, 1896). The number of glandular setae and the amount of toothing and lobing are very variable in this species; some collections (e.g. *Purpus 4050*) have the leaves eglandular and almost unlobed, while others have them copiously glandular-ciliate and conspicuously jagged-lobed. The type of *J. grandifrons* (*Conzatti & Gonzales 1206*, in Herb. Gray !) is an average mature specimen of the species. It should be noted that *J. ciliata* Muell. Arg. [Linnaea **34**: 209. 1865], a Peruvian species, must take another name because of the earlier *J. ciliata* Sessé. Several names are apparently available, including *J. Augusti* Pax & Hoffm., *J. Hoffmanniae* Croiz. [*J. longipedunculata* Pax & Hoffm.], and *J. Weberbaueri* Pax & Hoffm., but at

the present time it is impossible to ascertain the identities of these species and the points, if any, by which they differ from *J. ciliata* Muell. Arg.; it would be precipitate to rename the latter before thorough investigation of the group.

4. JATROPHA DIOICA Sessé apud Cerv. l.c.; König, l.c.; *Mozinna spathulata* Orteg. Dec. Pl. **8**: 105. *pl. 13.* 29 Ja, 1799; *Jatropha spatulata* Muell. Arg.

FIG. 1. The distribution of *Jatropha dioica* and allied species. Dots in the Gulf of California region (Sinaloa, Sonora, Baja California and Arizona) show the known occurrences of *J. cuneata* Wiggins & Rollins; dots east and south of this area, *J. dioica* var. *sessiliflora;* triangles, *J. dioica* var. *graminea;* oval, *J. neopauciflora.* The dots indicated by arrows refer to the intermediates (cited in the text) between var. *sessiliflora* and var. *graminea.* So far as known neither *J. cuneata* nor *J. dioica* crosses the Sierra Madre Occidental.

The map is based on specimens in the following herbaria: Arnold Arboretum, Field Museum, Gray Herbarium, New York Botanical Garden, United States National Arboretum, United States National Herbarium.

in DC. Prodr. **15**(2): 1081. 1866. The original description reads: "Jatropha (Dioica) floribus caliculatis dioicis, foliis oblongo spatulatis. Flor. Mex. cum icone." From this description, with its references to dioecism and oblong-spatulate leaves, this species may be referred confidently to *J. spathulata* or to *J. neopauciflora* Pax. The latter is known only from a small area near the border between Puebla and Oaxaca, whereas the former is the well-known "Sangre de Drago" (now often "sangregado") of the arid uplands of eastern and southern Mexico; the Sessé and Mociño specimen of *J. dioica* (no. 4238) is an ample (though sterile) one, unquestionably *J. spathulata*.

It is unfortunate that the well-known specific name *spathulata* is to be relegated to synonymy, but the case appears to be sufficiently clear. It should also be emphasized at this time that it seems impossible logically to uphold *Mozinna* as a genus distinct from *Jatropha*. The characters usually relied upon, those of the condensed inflorescence, fascicled cymes and leaves, and reduced number of carpels in *Mozinna*, break down completely when applied in contrast to the same characters in *Jatropha cordata*, *J. cinerea*, *J. cardiophylla* and other Mexican species. The sole remaining character is that of the leaf-shape, which is oblong to spatulate or obovate in *Mozinna* and mostly ovate-cordate in the related species of *Jatropha* proper; this character is scarcely of generic value, particularly as lobed or even cordate leaves appear occasionally in *Mozinna*, especially in very young or vigorous tissues.

Jatropha dioica may be readily divided into the following varieties and possibly into others; material is needed, from the region south of Mexico City, to determine the status of plants native to that part of the species' range:

1. Leaf-blades 2.5–6 times as long as wide, mostly 6–10 mm. wide ..... var. *sessiliflora*
1. Leaf-blades 6–17 times as long as wide, mostly 1–4 mm. wide ..... var. *graminea*

4a. JATROPHA DIOICA var. **sessiliflora** (Hook.) McVaugh, comb. nov. *Jatropha dioica* Sessé apud Cerv. l.c., as to type. *Mozinna spathulata* Orteg, l.c., as to type. *Loureira cuneifolia* Cav. Ic. **5**: 17. *pl. 429.* [late 1799]. *Mozinna spathulata* var. *sessiliflora* Hook. Ic. **4**: *pl. 357.* 1841. *Jatropha spatulata* var. *genuina* Muell. Arg. in DC. Prodr. **15**(2): 1081. 1866. *Jatropha spatulata* var. *sessiliflora* (Hook.) Muell. Arg. op. cit. 1082. *Zimapania Schiedeana* Engl. & Pax, Natürl. Pflanzenfam. III. **5**: 119. *f. 75.* 1891. *Mozinna sessiliflora* (Hook.) Small, Fl. SE. U. S. 706. 1903.

Leaves oblanceolate to obovate, (2.5) 3.5–5 (7) times as long as wide. Blades mostly 0.6–1 (1.8) cm. wide, 1.5–3.5 (7) cm. long, on shoots exceptionally 3 cm. wide, 4 cm. long, on a petiole 1 cm. long. Width of lobed blades, across the widest points of the lobes, 1.5–3.5 cm., the central lobe then 0.8–1.5 cm. wide.

The TYPE, *Hartweg 37*, from Zacatecas, is evidently an average specimen of this variety, as shown by Hooker's plate 357.

The specimens cited below are from the United States National Herbarium, the Herbarium of the National Arboretum, and the Field Museum; these are indicated by appropriate abbreviations. Where possible the flowering or fruiting condition of the specimen has been indicated also.

Specimens examined: TEXAS: Atascosa County: without locality, *Ellen D. Schulz 107*, Apr. 19, 1920 (fl, US). Bexar County: San Antonio, *J. N. Rose 24139*, Oct. 19, 1927 (US). Blanco County: Cañon Blanco, *J. Reverchon 1599*, June, 1875 (fr, US). Cameron County: Brownsville, *R. Runyon 243*, July, 1922 (fl, US). Green Island, *B. C. Tharp*, June 23–29, 1922 (fl, US). Nueces County: Corpus Christi, *A. A. Heller 1550*, Apr. 9–12, 1894 (fl, US), *H. C. Benke 5392*, Apr. 11, 1930 (fl, US). LaSalle County: Cotulla, *Louis Potter*, May 22, 1916 (USNA). Val Verde County: Mouth of the Pecos river, *V. Bailey 275*, May 21, 1900 (fl, US, 2 sheets). County undetermined: South Western Texas, *Ed. Palmer 1234* in 1879–80 (fl & fr, US).

TAMAULIPAS: Near Matamoros, *Berlandier 3210* in 1838 (US); Buena Vista Hacienda, *E. O. Wooton*, June 17, 1919 (US); San Fernando, *J. N. Rose 24323a*, Nov. 2, 1927 (US); Sierra de San Carlos, [Cerro de] la Tamaulipeca, vicinity of San Miguel, *H. H. Bartlett 10544, 10589*, July 24 and 26, 1930 (both F).

NUEVO LEÓN: Santa Catarina, [near] Monterrey, *Fr. Abbon 91* (Arsène 6244) July, 1911 (US); Lampazos, *Mary T. Edwards 375*, June 26, 1937 (F).

COAHUILA: Monclova, *E. W. Nelson 6747*, May 14, 1902 (US); Saltillo, *Ed. Palmer 226* in 1898 (USNA; some intermediate with var. graminea; 1/w about 7/1).

SAN LUIS POTOSÍ: Charcas, *C. L. Lundell 5506*, July–August, 1934 (F); San Luis Potosí market, *Ed. Palmer 612* in 1898 (fr, USNA); San Luis Potosí, *Ed. Palmer 31*, Aug. 18–20, 1902 (US, USNA); Smelter Hill, *C. R. Barnes & W. J. G. Land 106*, Sept. 20, 1908 (fr, F).

ZACATECAS: Pastorilla [i.e. Pastoría ?], *M. E. Jones 425*, May 2, 1892 (US); San Juan Capistrano, *J. N. Rose 3544*, Aug. 21, 1897 (US).

DURANGO: City of Durango, *Ed. Palmer 243*, [June 1–24], 1896 (fl, US).

GUANAJUATO: Empalme de Gonzales, *H. H. Rusby 40*, June, 1910 (US).

QUERETARO: Querétaro, *Bro. Agniel 7* (Arsène 10285), 1910–13 (US); *Bro. Agniel s.n.* (Arsène 10449), 1910–13 (fl, US); "Del Ciervo a Sn. Juan," *F. Altamirano 1754*, Aug. 27, 1905 (US).

HIDALGO: Jacala, *V. H. Chase 7336*, July 7, 1939 (F); Ixmiquilpán, *J. N. Rose 8927* in 1905 (US), *L. A. Kenoyer A629*, June 27, 1938 (fl, F); Pachuca, *G. L. Fisher 35499*, July 19, 1935 (fr, F, US); Tula, *Rose 4957*, June 8, 1899 (US).

DISTRITO FEDERAL: Guadalupe, valley of Mexico, *J. N. Rose 8506* in 1905 (US); Mont Zacoalco près Guadalupe, *Bourgeau 184*, June 8, 1865 (fl, US); Guadalupe prope Mexicum, *Née* (F).

PUEBLA: See note below.

OAXACA: See note below.

STATE UNDETERMINED: Valley of the Rio Grande below Doñana, *Parry et al.* (Mex. Bound. Surv. 1315) (fl, US); "New Mexico," *C. Wright 1812* in 1851–52 (US); Nova Hispania, *Sessé et al. 4238* ["1944"] in 1787–1804 (F; "Jatropha dioica N. ic."); 20 miles south of Nuevo Laredo, *C. H. & M. T. Mueller 446*, July, 1933 (F).

Note: Pringle 9391, from Tehuacán, Puebla, at 5500 ft., Aug. 7, 1901 (US) differs from var. *sessiliflora* in having the staminate sepals small (0.6–0.7 mm. long and wide), the corolla of 5 free strap-shaped petals 1 mm. wide, 3.5–4 mm. long, the lobes obtuse, not recurved, more or less densely puberulent on both sides, the 9 stamens about 4.5 mm. long, the outer loosely connate 2 mm., the inner connate 3 mm., the anthers 1 mm. long, the leaves up to 3 mm. wide, 21–27 mm. long, on definite petioles 1–1.5 mm. long, the veins reticulate with no evident lateral nerves, the old branches woody, apparently not fleshy, 2.5 mm. in diameter.

Conzatti (1473) & Vasquez, from Pueblo Viejo, Dto. Tlacolula, Oaxaca, at 1750 m., June 19–23, 1906 (US), has leaves up to 15 mm. wide, 30 mm. long, on definite petioles

2 mm. long, all obovate or a little narrower, the veins netted and with several fine lateral pairs, the pistillate sepals linear-elliptic, 1.5–2 mm. wide, 5 mm. long, scarious-margined, rounded at tip, nearly glabrous.

4b. JATROPHA DIOICA var. **graminea** McVaugh, var. nov.; folia anguste oblanceolata usque ad linearia, (6) 10–17-plo longiora quam latiora. Limbi plerumque 0.15–0.4 (0.65) cm. lati, 1–4 (8) cm. longi, cum lobati 1–1.5 (rare 4) cm. lati.

TYPE collected at Jimulco, Coahuila, at an elevation of 4200 ft., *Forrest Shreve 9419*, Sept. 14, 1939 (in the Herbarium of the National Arboretum).

Additional specimens examined: TEXAS: Brewster County: Boquillas, common, *H. C. Hanson 583*, April 17, 1919 (fl, US); Glenn Springs, *O. E. Sperry 603*, May 3, 1937 (fl, US); Chisos Mts., *C. H. Mueller* (herb. Univ. Tex. 8068), 7/10/31 (fr, US); Lajitas, *R. A. Studhalter 1074*, July, 1925 (fr, US). Presidio County: Presidio, *V. Havard*, Apr. 28, 188– (US).

COAHUILA: Mojada Mts., *M. E. Jones 424*, April 19, 1892 (fl, US); 25 miles west of El Oro, road to Guimbalete, *S. S. White 2015*, July 24, 1939 (fr, USNA); Jimulco, *C. G. Pringle 155*, Apr. 7 and Aug., 1885 (fl & fr, US); south of Saltillo, *R. Runyon 1330*, July 29, 1929 (US; intermediate with var. sessiliflora; l/w about 7/1).

CHIHUAHUA: Meoqui, *Harde LeSueur Mex 10*, August 29–30, 1935 (F); 13 mi. southeast of Saucillo, 4000 ft., *Shreve 8067*, July 29, 1937 (fr, F, US); vicinity of Chihuahua, *Ed. Palmer 125*, Apr. 8–27, 1908 (fl, US); State of Chihuahua [at or near the city of Chihuahua, according to Rose's field-book], *J. N. Rose 4929*, May 11, 1899 (US).

ZACATECAS: Vicinity of Cedros, *J. E. Kirkwood 26*, in 1908 (fr, F); footslopes and their ridges, Cedros, *F. E. Lloyd 146*, Aug., 1908 (fl & fr, US).

SAN LUIS POTOSÍ: Locality unknown, *C. C. Parry & Ed. Palmer 830* in 1878 (fl, US; this approaches var. sessiliflora; l/w mostly 4–6.5/1).

STATE UNKNOWN: Valley of the Rio Grande below Doñana, *Parry et al.* (Mex. Bound. Surv. 1315a) (fr, US).

5. JATROPHA PALMATA Sessé apud Cerv. l.c.; König, l.c. The original description reads: "Jatropha (Palmata) Floribus caliculatis, foliis cordatis lobatis denticulato ciliatis. Flor. Mexic." The material under this name in the Sessé and Mociño herbarium (no. 4230) is evidently a species of *Manihot*, with glabrous ovary, glabrous 3- or 5-lobed leaves, the lobes broad, ovate or elliptic, acuminate, entire. The material is too scanty for positive identification, but suggests *M. aesculifolia* (H.B.K.) Pohl. In any event the name cannot be transferred to *Manihot* because of the existence of *M. palmata* (Vell.) Muell. Arg. It should be noted also, however, that the original description of *Jatropha palmata* as given above does not agree with the specimens at hand, or with the characters of *Manihot* in general; "floribus caliculatis" could hardly refer to any *Manihot*, and "foliis . . . denticulato ciliatis" certainly does not refer to the plants under no. 4230. The identity of *Jatropha palmata* cannot be definitely established.

6. JATROPHA TRILOBA Sessé apud Cerv. l.c.; König, l.c. The original description reads: "Jatropha (triloba) floribus excaliculatis, foliis trilobis acuminatis, integerrimis. Flor. Mex. Hucipochotl Hernandez edit. Roman. 61. Matritens. Tom. 2. p. 361." The plant under this name in the herbarium (no.

4228) is a sterile specimen which agrees exactly in foliar characters with the flowering specimens of *Manihot foetida* comprising no. 4229 and with the plate of *Jatropha triloba* in the Delessert Herbarium (Field Mus. neg. 30857), which seems likewise to represent *M. foetida*, and there seems to be no reason to doubt that *Jatropha triloba* and *Manihot foetida* are identical. The latter species, however, is known only from the original collection, and until it is possible to make an examination of the type it would be precipitate to take up Sessé's name for it, so that I am not transferring it to *Manihot* at this time.

Cervantes' reference to Hernández was evidently ill-founded, for the figure in the 1651 Roman edition of the "Rerum Medicarum" appears to portray *Jatropha gossypifolia;* the calyx and corolla are both clearly shown, as are the numerous flowers and the alternate branching characteristic of the inflorescence of this species; in Hernández' description, moreover, the plant is said to be decumbent or scandent, with scarlet flowers; the principal similarity between *Jatropha triloba* and the plant figured by Hernández is in the leaves, which in both cases have three entire lobes.

7. JATROPHA QUINQUELOBA Sessé apud Cerv. l.c.; König, l.c. The description reads: Jatropha (Quinqueloba) floribus excaliculatis foliis quinquelobis oblongo ovatis integerrimis. Flora Mex." The herbarium material of this species (no. 4227) appears to agree in every detail with the Sessé & Mociño specimen cited by Mueller Argoviensis as his *Jatropha tubulosa* var. *septemloba* (specimen in the Boissier Herbarium, Field Mus. neg. 24392); the similarity in general characters of leaf and inflorescence is so striking that I should suppose both specimens to have come from the same plant. Mueller's specimen may also be considered as the type-specimen of *J. tubulosa*. He cited no specimens under the inclusive species *tubulosa*, but only under the several varieties: var. α *septemloba*, var. β *quinqueloba*, var. γ *triloba*. Since Mueller designated no variety *genuina* (as was his usual custom), we may arbitrarily select var. *septemloba*, his first variety, as the most representative of his species; var. *quinqueloba* seems to have been a mixture, perhaps of more than two varieties or species, and var. *triloba* was based on a single specimen, supposedly from Peru where no plants of this affinity are known to occur.

The type-sheet of *J. tubulosa* var. *quinqueloba* (in the Delessert Herbarium, represented by Field Mus. neg. 24391) bears not only the Andrieux specimen cited by Mueller but also a leaf which appears to be that of one of the more densely hairy forms of *J. tubulosa* and which is accompanied by a typical Sessé and Mociño notation: "Jatropha quinqueloba N[ueva] E[spaña]." At least two of Mueller's three varieties of *J. tubulosa* are thus based at least in part on material of *J. quinqueloba* Sessé. If the type of var. *septemloba* be regarded as the type of *J. tubulosa* as well, then Mueller's

species is based directly upon *J. quinqueloba*, which is thus the valid name for the plant if it is considered a *Jatropha*. Happily for stability in nomenclature, the name *quinquelobus* is preoccupied in *Cnidoscolus* to which it seems necessary to refer this species; its proper designation here is *Cnidoscolus tubulosus* (Muell. Arg.) Johnston.

8. JATROPHA OCTANDRA Sessé apud Cerv. l.c.; König, Tracts Bot. 232. 1805. The description reads: "Jatropha (octandra) floribus excaliculatis octandriis, foliis palmatis, lobis intermediis hastatis. Flor. Mex. cum icone." This is apparently a *Cnidoscolus*, but no material of it was found in the herbarium, and its identity is indeterminable from the description alone.

SUMMARY

On the basis of specimens in the herbarium of Sessé and Mociño, it is possible to establish the identity of *Jatropha edulis*, *J. ciliata*, *J. dioica*, *J. triloba*, and *J. quinqueloba*, all species described by Sessé in a paper by Cervantes in 1794. The typification of *J. peltata* Sessé and *J. palmata* Sessé is hardly possible on the basis of the material available. The identity of *J. octandra* Sessé, of which no material is available, is unknown. *Jatropha heterophylla* Sessé & Mociño and *J. moluensis* Sessé & Mociño are typified by specimens in the collection.

The following new names are proposed: *Jatropha Humboldtiana*, *J. dioica* var. *sessiliflora*, *J. dioica* var. *graminea*. The following are relegated to synonymy: *Jatropha peltata* H.B.K., *J. edulis* Sessé, *J. yucatanensis* Briq., *J. olivacea* Muell. Arg., *J. grandifrons* Johnst., *J. spathulata* (Orteg.) Muell. Arg., *J. quinqueloba* Sessé.

DIVISION OF PLANT EXPLORATION AND INTRODUCTION,
BUREAU OF PLANT INDUSTRY STATION
BELTSVILLE, MARYLAND

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 72, NO. 1, pp. 42–46 JANUARY, 1945

JUNIPERUS VIRGINIANA, J. HORIZONTALIS, AND J. SCOPULORUM—III. POSSIBLE HYBRIDIZATION OF J. HORIZONTALIS AND J. SCOPULORUM

NORMAN C. FASSETT

Of the several differences between *Juniperus horizontalis* and *J. scopulorum*,[1] four have been chosen as most conveniently dealt with. Table 1 shows a survey of a mass collection from Bridger, Montana, where each individual is erect, with a foliar gland exceeding in length the distance from the gland to the tip of the leaf, with obtuse leaf tips, and with 11–60 per cent of the fruiting peduncles hooked; in other collections of this species they run from 8–70 per cent hooked. Table 2 shows a similar survey of a mass collection of *J. horizontalis*, from a locality about 100 miles to the east of that represented in table 1, on the other side of the Big Horn Mountains. In this collection, every individual is creeping, with foliar gland shorter than the distance from the gland to the tip of the leaf, the leaf tips are apiculate, and 75–100 per cent of the fruiting peduncles are hooked; this last figure may run as low as 70 per cent in other collections. Just across the road from the colony of *J. horizontalis* treated in table 2, is a patch of cedars, obviously *J. scopulorum*. When analyzed, however, they show (table 3) certain tendencies in the direction of the neighboring species, for the foliar gland is sometimes shorter than the distance to the leaf tip, the leaf tips are sometimes acute or even slightly apiculate, and the percentage of hooked peduncles runs higher than is normal for *J. scopulorum*. It appears, then, that in this case *J. horizontalis* is showing some influence on *J. scopulorum*, but *J. scopulorum* is showing no influence on *J. horizontalis*.

TABLE 1. *Ten individuals of J. scopulorum from Bridger, Montana*

Habit	Gland shorter than distance to tip of leaf, or longer	Leaf tips	Per cent of peduncles curved
Erect	Longer	Obtuse	.....
Erect	Longer	Obtuse	19
Erect	Longer	Obtuse	11
Erect	Longer	Obtuse	11
Erect	Longer	Obtuse	.....
Erect	Longer	Obtuse	.....
Erect	Longer	Obtuse	60
Erect	Longer	Obtuse	47
Erect	Longer	Obtuse	.....
Erect	Longer	Obtuse	33

[1] Bull. Torrey Club 71: 410–418. 1944.

TABLE 2. *Nine individuals of J. horizontalis from 5 miles north of Sheridan, Wyoming*

Habit	Gland shorter than distance to tip of leaf, or longer	Leaf tips	Per cent of peduncles curved
Creeping	Shorter	Apiculate	.....
Creeping	Shorter	Apiculate	100
Creeping	Shorter	Apiculate	100
Creeping	Shorter	Apiculate	100
Creeping	Shorter	Apiculate	75
Creeping	Shorter	Apiculate	.....
Creeping	Shorter	Apiculate	.....
Creeping	Shorter	Apiculate	.....
Creeping	Shorter	Apiculate	88

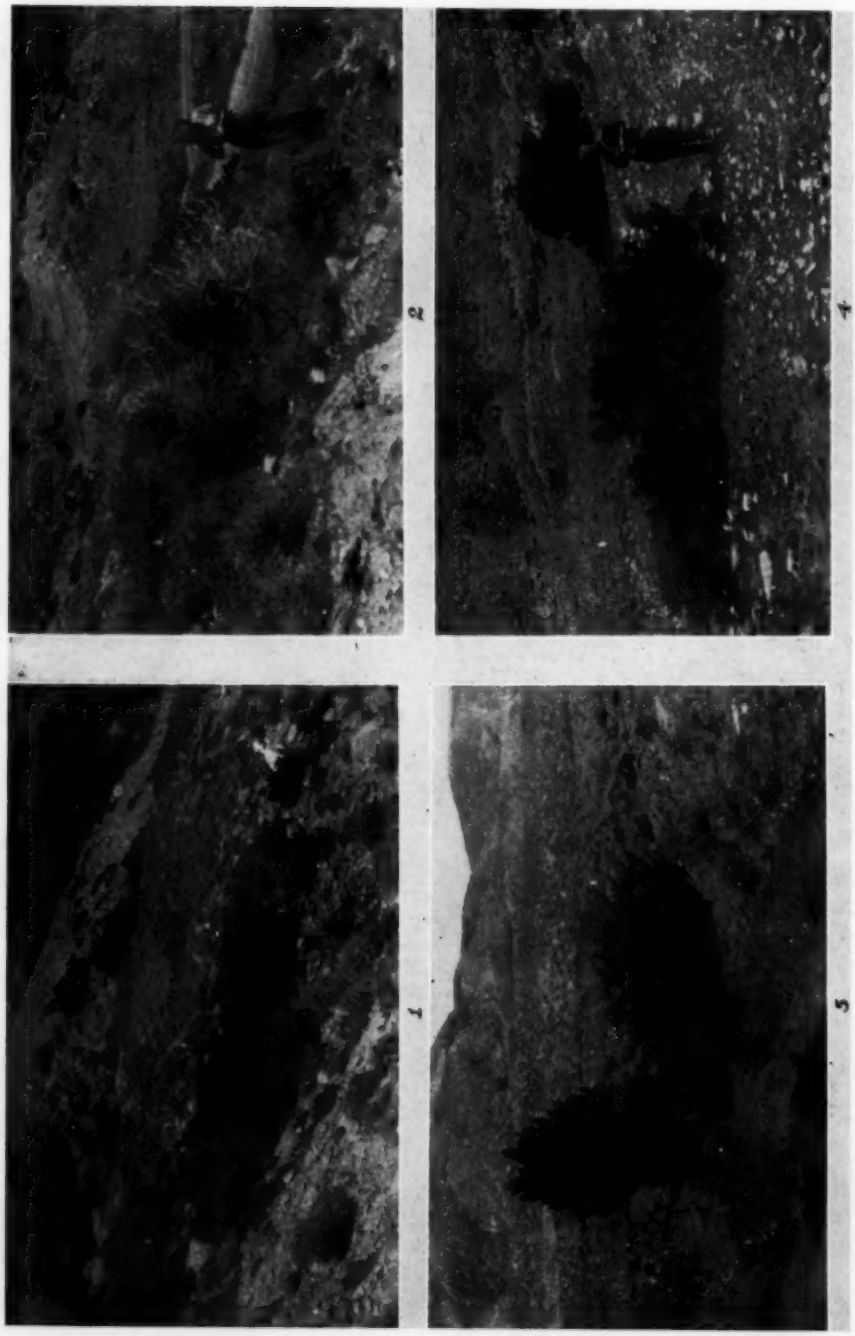
About 20 miles west of this point, near Steamboat Rock on the east slope of the Big Horn Mountains, six individuals of *J. horizontalis* were found; they, likewise, showed no characters suggesting influence of *J. scopulorum*.

The west slopes of the Big Horn Mountains are covered with great masses of red cedar (figs. 1–2), and these extend westward over the plains for about ten miles from the foot of the mountains (figs. 3–4). Many of the plants are erect and seem to be good *J. scopulorum* except for the slightly high proportion of hooked peduncles (table 4), while other plants are depressed, with about the general habit of the eastern *J. communis* var. *depressa*. In some cases, both types appear together (table 4; fig. 3), while in others the depressed form alone occurs (table 5).

No *J. horizontalis* was observed in the region; that the depressed habit of the *J. scopulorum* is due to hybridization with that species is highly conjectural. It must be noted that the populations on the west slopes of the Big Horns and on the adjacent plains consist of two relatively constant types,

TABLE 3. *Ten individuals of a hybrid swarm of J. scopulorum and J. horizontalis from 5 miles north of Sheridan, Wyoming*

Habit	Gland shorter than distance to tip of leaf, or longer	Leaf tips	Per cent of peduncles curved
Erect	Shorter	Obtuse	92
Erect	Shorter	Obtuse	.....
Erect	Longer	Obtuse	74
Erect	Both	Obtuse	75
Erect	Both	Acute	56
Erect	Longer	Obtuse	78
Erect	Longer	Obtuse	72
Erect	Longer	Obtuse	76
Erect	Shorter	Obtuse but minutely apiculate	.....
Erect	Longer	Obtuse	.....



FIGS. 1, 2. *Juniperus scopulorum* var. *patens* on the west slopes of the Big Horn Mountains, along highway Wyoming 14, near the western edge of Big Horn National Forest. FIG. 3. *J. scopulorum* (left) and *J. scopulorum* var. *patens* (right) on plains west of Big Horn Mountains. FIG. 4. *J. scopulorum* var. *patens* on plains west of Big Horn Mountains.

TABLE 4. *Fourteen individuals of J. scopulorum and J. scopulorum var. patens from the plains between the Big Horn River and the Big Horn Mountains, east of Lovell, Wyoming*

Habit	Gland shorter than distance to tip of leaf, or longer	Leaf tips	Per cent of peduncles hooked
Depressed	Longer	Obtuse	72
Depressed	Longer	Obtuse	72
Depressed	Longer	Obtuse	.....
Depressed	Longer	Obtuse	.....
Depressed	Longer	Obtuse	.....
Depressed	Longer	Obtuse	.....
Depressed	Longer	Obtuse	.....
Depressed	Longer	Obtuse	.....
Depressed	Longer	Obtuse	.....
Depressed	Shorter	Acute	.....
	(Semijuvenile foliage)		
Erect	Longer	Obtuse	91
Erect	Longer	Obtuse	.....
Erect	Longer	Obtuse	38
Erect	Longer	Obtuse	.....

differing only in habit. This is in marked contrast to the purported hybrid colony represented by table 3, where three of the characters of *J. horizontalis* had more or less infiltrated a colony of *J. scopulorum*, and in extreme contrast to the hybrid colonies[2] of *J. virginiana* and *J. scopulorum*, which showed a multitude of recombinations of the characters of the two parent species.

If these depressed individuals of *J. scopulorum* are actually the product of a cross with *J. horizontalis*, they are not the result of any recent hybridization, but rather of some ancient gene flow from one species into the other. In any case, it is a fact that such individuals are characteristic of certain

TABLE 5. *Twelve individuals of J. scopulorum var. patens from the west slope of the Big Horn Mountains, east of Lovell, Wyoming*

Habit	Gland shorter than distance to tip of leaf, or longer	Leaf tips	Per cent of peduncles hooked
Depressed	Longer	Obtuse	48
Depressed	Longer	Obtuse	.....
Depressed	Longer	Obtuse	50
Depressed	Longer	Obtuse	.....
Depressed	Longer	Obtuse	53
Depressed	Longer	Obtuse	.....
Depressed	Longer	Obtuse	74
Depressed	Longer	Obtuse	70
Depressed	Longer	Obtuse	.....
Depressed	Longer	Obtuse	.....
Depressed	Longer	Subacute	50
Depressed	Longer	Obtuse	57

[2] Bull. Torrey Club 71: 475–483. 1944.

localities within the range of *J. scopulorum*. This phase of the species may, for convenience, be called:

J. SCOPULORUM Sarg. var. **patens** Fassett, var. nov. Plantae circa 1 m. altae, patentes. WYOMING: between the Big Horn River and the Big Horn Mountains, east of Lovell, June 24, 1941, *N. C. Fassett 22062* (TYPE in Herb. Univ. of Wis.); west slope of Big Horn Mountains near Lovell, June 24, 1941, *Fassett*, many numbers. The following collections are in the Arnold Arboretum. WYOMING: Big Horn Mts., 6400 ft. alt., on road Sheridan to Dome Lake, Sept. 1, 1900, *J. G. Jack* [foliage of *J. scopulorum*, but labelled "*Juniperus Sabina, procumbens*"]. ALBERTA: Devil's Head Lake, Lat. 51° 15′, Long. 115° 25′, Banff, July 6, 1891, *Macoun* [foliage of *J. scopulorum*, but labelled "*Juniperus Sabina* var. *procumbens*"]; dry slopes, Banff, Aug. 9, 1904, *Alfred Rehder*, "spreading shrub, ½–1 m.; foliage yellowish green"; same data but "foliage bluish green"; Banff, August 9, 1897, *C. S. Sargent*, "small plant, rare."

The advisability of naming hybrids has recently been discussed by Camp & Gilly;[3] the case of *J. virginiana* and *J. scopulorum*[4] is like that of *Vaccinium atrococcum* and *V. Torreyanum*, with a heterozygous population in which it is not practicable to apply names to the various elements, while the hybrids of *J. scopulorum* and *J. horizontalis* (if indeed they are hybrids of those species) appear as a more homogeneous population of decumbent shrubs with the foliage identical with or similar to that of *J. scopulorum*, and only occasionally approaching that of *J. horizontalis*.

The writer is indebted to the Wisconsin Alumni Research Foundation for travel funds to study these plants in Wyoming, and to the curators of the Gray Herbarium and of the Arnold Arboretum for loans of herbarium material.

SUMMARY

When *Juniperus scopulorum* and *J. horizontalis* occur together, there are several things that may happen. Near Sheridan, Wyoming, the two species occur on opposite sides of a road; *J. scopulorum* shows tendencies toward *J. horizontalis* in several characters, but *J. horizontalis* shows no characters of *J. scopulorum*. On the west slopes of the Big Horn Mountains, Wyoming, and on the adjacent plains, where no *J. horizontalis* was observed, and in the vicinity of Banff, Alberta, where the writer has not had opportunity to make field studies, occurs a depressed shrub with the foliage and fruit of *J. scopulorum*, which is described as *J. scopulorum* var. *patens*, var. nov.; it is suggested that this variety may have arisen by some ancient hybridization of *J. scopulorum* with *J. horizontalis*.

DEPARTMENT OF BOTANY, UNIVERSITY OF WISCONSIN
MADISON, WISCONSIN

[3] Brittonia **4**: 362–363. 1943.
[4] Bull. Torrey Club **71**: 475–488. 1944.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 72, NO. 1, PP. 47–51 JANUARY, 1945

RHIZIDIOMYCES HIRSUTUS SP. NOV., A HAIRY ANISOCHYTRID FROM BRAZIL

JOHN S. KARLING

Anisochytrids are simple fungi with anteriorly uniflagellate zoospores, which resemble the true chytrids in structure and development, but because of the anterior position of the flagellum on the zoospores they have been separated from the Chytridiales and segregated by the author[1] in another order, the Anisochytridales. They are comparatively few in number as far as is now known and up to the present time less than a score of species have been recorded in mycological literature.

In a previous publication relating to aquatic fungi of the Amazon Valley in Brazil the author[2] reported the occurrence of two known anisochytrids, *R. apophysatus* and *R. bivellatus*, in South America and described a third species, *R. Hansonae*, which was isolated from moist soil samples collected at San Carlos, Matto Grosso and in Manaus, Amazonas. Since that time a fourth species of the same genus has been found in moist leaf mold[3] from Seringal Monte Alegre about sixty miles southeast of Rio Branco in Acre Territory. This species differs primarily from the known members of *Rhizidiomyces* by the presence of numerous elongate coarse hairs on the surface of the sporangia. Otherwise, it is non-apophysate and saprophytic like *R. bivellatus* and *R. Hansonae*, with large zoospores of about the same size as those of *R. bivellatus*. The hirsute character of the sporangia, however, clearly distinguishes this Brazilian fungus from the other species of *Rhizidiomyces*, and it is accordingly regarded by the writer as a new species for which the name *R. hirsutus* is proposed.

Rhizidiomyces hirsutus Karling, sp. nov. Sporangiis extramatricalibus, non apophysatis, hyalinis, globosis (6–180 μ diam.), ovalibus (8–20 × 20–60 μ), pyriformibus, obpyriformibus, oblongis, aut irregularibus, 3–47 setis elongatis crassis (15–190 μ longis, 2–3 μ latis) munitis. Zoosporis ovalibus, oblongis, aut elongatis, 3–4 × 6–8 μ, unam pluresve granulas minutas refringentes habentibus; flagello 14–18 μ longo. Systemate rhizoideo valde ramoso, pro more monoaxiali, e basi sporangii orto thallo in substrato solido crescenti, saepe e locis pluribus orto et visu leviter radiali thallo in media liquida crescenti.

[1] **Karling, J. S.** 1943. The life history of *Anisolpidium Ectocarpii* gen. nov. et. sp. nov., and a synopsis and classification of other fungi with anteriorly uniflagellate zoospores. Am. Jour. Bot. **30**: 637–648.

[2] ————. 1944. Brazilian anisochytrids. Ibid **31**: 391–397.

[3] The writer is grateful to Dr. J. T. Baldwin for collecting the leaf mold on one of his trips to the Acre Territory.

Saprophytic in moist leaf mold, Seringal Monte Alegre, Acre Territory, Brazil.

This species was first isolated on bits of hemp seed, but has since been grown successfully on bits of corn and grass leaves, onion skin, insect exuviae, chitin, pollen grains of numerous Angiosperms, synthetic agar media and in liquid media. However, the best and most abundant growth occurs on hemp seed where the sporangia and surface hairs attain their greatest diameter and length. When grown on this substratum, the young and mature sporangia are usually filled with refractive bodies of various sizes (figs. 15–17) which may be so numerous and closely crowded that they often become angular in shape. Occasionally, the refractive bodies may even occur in the rhizoids and sporangial hairs (figs. 17, 18). These refringent bodies are blackened by osmic acid, indicating that they are of an oily composition.

Although *R. hirsutus* grows readily as a saprophyte on various substrata and synthetic media, it may occasionally infect the oogonia of *Achlya flagellata* when the two fungi are grown together on hemp seeds. In such cases the sporangia of the parasite resemble somewhat those of *R. apophysatus* which may also be spiny, according to Zopf,[4] and infect the same host. However, the length and coarseness of the hairs on the sporangia as well as the large zoospores produced by *R. hirsutus* distinguish it quite clearly from this species.

The usual method of development of *R. hirsutus* is so similar to that of *R. bivellatus* and *R. Hansonii* that it is not necessary to describe it in detail. The present description will accordingly be limited largely to differences and variations of this process. However, it may be noted first that in the normal developmental cycle, the zoospores (figs. 2, 3), which usually contain one fairly large and several smaller granules, come to rest (fig. 4) and develop one or more germ tubes which penetrate the substratum (fig. 5). Shortly after this has occurred, small buds appear on the surface of the spore and elongate into filaments (fig. 15) and later become the sporangial hairs. The germ tube branches and gradually develops into the rhizoidal system (fig. 16), while the extramatrical spore body enlarges and becomes the sporangium. At maturity the thallus of *R. hirsutus* has the structure and appearance shown in figure 1. The exit tube then begins to develop as a broad, more or less hyaline papilla (fig. 1) and elongates to from 8 to 60 μ as the sporeplasm slowly moves upward. As this upward flow of protoplasm continues, the tube expands at the tip (fig. 12), and finally the entire content of the sporangium passes out and undergoes cleavage into zoospores (figs. 13, 14). As in other species of *Rhizidiomyces* described by the author, the

[4] **Zopf, W.** 1884. Zur Kenntniss der Phycomyceten. Nova Acta Leop.–Carol. Akad. 47: 188.

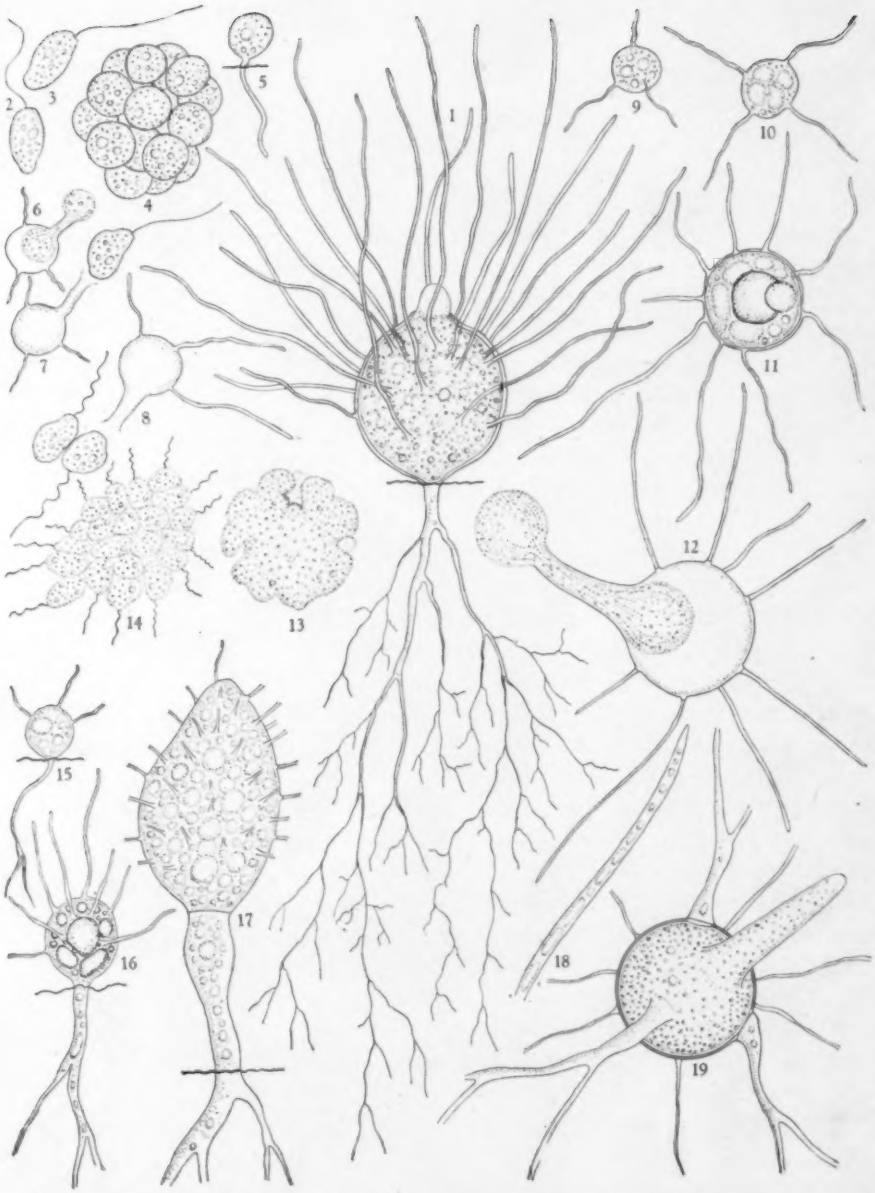


FIG. 1. Mature thallus of *R. hirsutus*. ×600. FIGS. 2, 3. Zoospores with one fairly large and several minute granules. ×1000. FIG. 4. Mass of quiescent spores. ×1000. FIG. 5. Germination of spore on a solid substratum. ×1000. FIG. 6. Emergence of the protoplasm of a spore or minute sporangium with three short setae. ×1200. FIG. 7. Later stage showing protoplasm transformed into a zoospore. ×1200. FIG. 8. Slightly larger sporangium which has formed two zoospores. ×1200. FIGS. 9, 10, 11. Stages in the development of extramatrical thalli growing in a liquid medium; peripheral hairs functioning as rhizoids. ×1000. FIG. 12 Emergence of protoplasm. ×1000. FIGS 13, 14. Cleavage of protoplasm into zoospores. ×800. FIGS. 15, 16. Successive stages of thallus development on a solid substratum. ×1000. FIG. 17. Sporangium with broken hairs. ×1000. FIG. 18. Enlarged portion of a sporangial hair containing numerous refractive bodies. ×1800. FIG. 19. Extramatrical thallus with rhizoids and sporangial hairs. ×1000.

emerged protoplasmic mass appears to be naked, and no vesicular membrane has been observed around the zoospores.

As was noted earlier, the sporangial hairs begin as small buds on the surface of the enlarging spore body, and in the early stages they are almost indistinguishable from germ tubes except for their smaller diameter. On large mature sporangia they may become 190 μ long and from 2 to 3 μ in diameter. As far as present observations go, the hairs rarely branch, but they often contain several rod-shaped, oval, and globular refractive bodies (fig. 18). In contaminated hemp seed and other cultures, numerous protozoa, rotifers and other microscopic animals are often present, and these may crawl and feed back and forth over the sporangia. In such cases the sporangial hairs often break off and leave short stubs on the surface of the sporangia, as shown in figure 17.

Numerous variations and abnormalities of the above described developmental cycle occur. Quite often the zoospores fail to become actively motile and round up after a brief period of rocking movement. As a consequence, loose masses of quiescent spores frequently occur (fig. 3) which resemble the cystospores of higher Phycomycetes. These spores may disintegrate or germinate directly in water without coming into contact with a solid substratum. In a few cases observed, such spores developed short hairs and an exit tube and formed a zoospore without further growth. Figure 6 shows a spore or minute sporangium the content of which is emerging through a short exit tube. The discharged protoplasm then developed without cleavage into a normal-sized zoospore (fig. 7), which became flagellate and swam away. The emergence of protoplasm from such spores and its transformation into zoospores do not differ fundamentally from the changes involved in diplanetism in higher Phycomycetes. A slightly larger spore or sporangium is shown in figure 8, from which the content has emerged and divided into two normal zoospores.

In synthetic liquid media the spores may form hairs and develop into fairly large thalli without forming rhizoids (figs. 9–12). In such thalli the tenuous hairs apparently function as absorbing organs and take the place of rhizoids in this physiological function, because the incipient sporangia grow in size, mature, and form zoospores in the normal manner (figs. 12–14). From other completely extramatrical thalli, definite rhizoids may develop in addition to sporangial hairs (fig. 19). The rhizoids of these thalli often arise at several points on the surface of the sporangium, branch freely, and extend somewhat radially in the surrounding liquid medium. Except for their hyaline color, such thalli resemble the extramatrical polyrhizoidal ones described by the author in *R. bivellatus*.

In large abnormal sporangia the exit tube may attain a length of 170 μ and branch one or several times. In such cases, the protoplasm is often used

up in exit-tube development and becomes so dispersed that no zoospores are produced. Abnormal sporangia with as many as from two to four exit tubes may also occur in *R. hirsutus*. Sometimes the protoplasm fails to emerge through the exit tube, with the result that cleavage and development of zoospores may occur within the sporangium. Such zoospores, however, do not usually become motile. In other cases observed, part of the protoplasmic mass remained in the sporangium and underwent cleavage into zoospores which became motile and later escaped singly through the exit tube. Occasionally, cleavage may be incomplete or unequal so that large bi-, tri-, and tetra-flagellate zoospores are formed.

So far no resting spores or dormant thick-walled sporangia have been found, and it is not known by what means *R. hirsutus* is able to survive unfavorable environmental conditions.

SUMMARY

Rhizidiomyces hirsutus sp. nov. was isolated on hemp seed from moist leaf mold collected at Seringal Monte Alegre in Acre Territory, Brazil. It grows well as a saprophyte on various solid vegetable and animal substrata, synthetic agar, and in synthetic liquid media, but may occasionally parasitize the oogonia of *Achlya flagellata* when grown together with this fungus on hemp seed. It differs primarily from other species of *Rhizidiomyces* by the presence of numerous long coarse hairs on the surface of the sporangia and by the production of large zoospores. No resting spores or dormant sporangia have been found.

BOTANY DEPARTMENT, COLUMBIA UNIVERSITY
NEW YORK

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 72, NO. 1, PP. 52–75 JANUARY, 1945

HISTORY AND NOMENCLATURE OF THE HIGHER UNITS OF CLASSIFICATION

LEON CROIZAT

Immediate taxonomic needs have repeatedly forced me to consult the prefaces of the works of Linnaeus, Adanson, Haller, Necker, Ventenat, Lamarck, A. L. de Jussieu, Jaume-St. Hilaire, A. de Jussieu, Robert Brown, Lindley, and other less well-known botanists. As a byproduct of these consultations I have collected certain notes which are interesting for the history of botanical thought in general, and even more valuable, I believe, as an elucidation of much that is obscure about the origin and nature of systematic units above the genus. To be informed about history may rate as an amenity, but to handle these units with purposeful understanding is a necessity. How little we know about them is revealed by a glance through the pages of so widely consulted a reference as the *Natürlichen Pflanzenfamilien,* 2nd edition. In one volume (op. cit. **21.** 1925) Gilg, Pilger, and Melchior follow different standards in presenting the synonymy of the Ochnaceae, Caryocaraceae, and Violaceae, only that the last family being so some extent satisfactory.

This study must be brief; it acquaints the reader with certain works which it proves essential to appraise and to know, but makes no claim to being exhaustive. The student of any form of thought reckons with the fact that thought does not form itself of a sudden, but many are the rivulets which build the head of the stream. No doubt, the inception of true, or natural classification may be carried back at least to the days of Caesalpin. To delve that far back, and to check each strand to its prime source, is definitely not the purpose of this study. To fulfill its aims, I believe, this study needs but to consider the lapse of a century, between 1735 and 1835. Within these hundred years natural classification was born, brought to flower, and mostly elaborated in the nomenclatural sense.

DESCRIPTION VS. INTERPRETATION

Hardly anything can be understood unless its inmost parts are digested and brought forth in as simple a manner as possible. Nature is full of facts, and history is bespangled with dates, but merely to record them serves little purpose. To grasp the subject with which we are about to deal, let us suppose that, clad in pelts and brought back to an untutored age, we face the world of vegetables. Some plants we can use, others we cannot. Some give health, others destroy it. Almost of necessity, our first classification will tend to divide the plants around us into the useful and the noxious. Later on,

having mastered writing, we will make certain that our descendants shall profit from our knowledge by *describing* these plants under chapters such as "Plants with roots that can be eaten," "Herbs which are good in love-potions and magic brews," and the like. We may, of course, take into account the fact that some of these plants are tree-like and perennial, others fugacious weeds.

As time wears off, and our grasp of nature becomes more self-conscious and firmer, we will give ourselves some account of the fact that certain groups, like the leguminous, characterized by common kinship, may well happen to include trees, shrubs, and herbs, and be useful or not for immediate material needs. By investigating these groups as something somehow related, we shall perceive that, while they may be much alike in fruit, they may differ in flower and foliage, or the other way around. Almost unconsciously, we shall be drawn to use these characters in order to arrange the plants which we describe within certain groups, clans, or tribes. By so doing we will implement our descriptions with *artificial keys*. If, mistaking these keys as true classification, we rely on the compound nature of the foliage to associate *Gymnoclados* with *Cladrastis*, excluding *Cercis;* on the papilionaceous corolla to place together *Cladrastis* and *Cercis*, ruling out *Gymnoclados;* on the male ament to set up as one unit *Populus*, *Salix*, *Carpinus*, *Corylus*, *Quercus*, *Juglans*, *Carya*, and *Myrica;* we shall write an *artificial classification*.

As a final stage in our botanical toils, and with the world as our province, we shall realize that no amount of laborious describing or keying avails us to put together *Hura crepitans* and *Euphorbia obesa*, for these plants are altogether unlike in body, fruit, and flower. After much thought, and through a careful study of true relationships, we shall soar to the perception of a quivering, evolutionary knot of life which binds *Hura* and *Euphorbia*. This knot we shall refer to as the Euphorbiaceae; we shall feel competent to describe its characters, more or less adequately—for indeed there are none—only after we shall have thought ourselves out. At this stage we shall have reached a *natural classification*.

Since human thought runs in channels, although some men are far in advance of others, it is not to be expected that rudimentary botany, artificial botany, and natural botany have parted company of a sudden. Transitional stages have connected these three brands of botany, the conservative and the unimaginative being forever fated to fight against the progressive and the imaginative.

It will readily be seen that great historical significance attaches to a work, regardless of its length or acknowledged purpose, in which an author begins to give himself *conscious account* of new facts and needs, and begins to act *deliberately* in order to meet them. The precursor, whose thought is

not always conscious, and whose actions are not necessarily deliberate, may thus happen to yield in the estimation of mankind to the vulgarizer, who is able to pass new ideas on to others ready for elaboration and immediate use. Service, obviously, is the earmark of true genius.

This study is not concerned with the transitional stage[1] which has connected rudimentary botany with artificial botany, but only with certain steps that have connected artificial classification with natural classification. These crucial steps have been taken by comparatively few authors, often in short pages. He who clearly began to see that puttering with certain characters of the corolla and of the stamens could yield only endless schemes of artificial classification, that is, nothing better than artificial keys, and to understand that artificial keys are not true botany, is to our science what the discoverer of the symbol zero is to mathematics. Once we know these creative souls, and have their statements before our eyes, we are provided with a safe yardstick to measure progress, and to judge of services rendered. We can readily weigh Adanson's work against Necker's, despite superficial resemblances which may induce some to dismiss both these men as crackpots. The pedagogical value attaching to the possession of such a yardstick will be apparent to an imaginative teacher, whose problem is to quicken the best in the minds of youth.

LINNAEUS, ADANSON, HALLER, AND GLEDITSCH

In 1735 a thin folio came out of the press in which a young man, known to us as Linnaeus, set forth certain generalities about the three classic kingdoms of nature. In this work, the *Systema Naturae*, Linnaeus introduced a schematic arrangement of the world of vegetables with some plain figures. This arrangement is titled "Clavis Systematis Sexualis," and begins: "Nuptiae Plantarum. Actus generationis incolarum Regni Vegetabilis, *Florescentia.*" This is followed, wholly in the manner of a modern taxonomic key, by two divisions, reading: "Publicae. Nuptiae coram totum mundum

[1] Rudimentary botany held its own to within half a century before the beginnings of natural classification. Ray's *Methodus Plantarum* (1682), though enriched by remarkable studies on the structure of the seed, is still remote from anything heralding the new era, and, as Ray himself admits (Meth. Pl. Emend. Dedicatio [3] 1703), was held in contempt by contemporary botanists. It is difficult indeed to believe that groups formed by *Ulmus, Fraxinus, Acer, Carpinus,* and *Tilia,* or by *Chelidonium, Ranunculus, Malva,* and *Fragaria* can be the modern Orders as suggested by the most recent bibliographer of Ray (Raven, *John Ray Naturalist, His Life Works,* 194. 1942). The speed at which botany could progress at this period, however, is nowhere better documented than in Ray's *Methodus Plantarum Emendata* (1703). This work bears witness to his greatness as a progressive thinker. Aside from its introduction of the Monocotyledons and Dicotyledons, its contributions to nomenclature, and its excellent discussion of generalities, Ray's second *Methodus* may easily lay claim to have begun classification by families in its treatment of the liliaceous and graminaceous alliances. Ray holds a position of preëminence among the forerunners of natural classification, and ranks very high among botanists and naturalists of creative ability.

visibilem aperte celebrantur. *Flores unicuique visibiles sunt,*" "Clandestinae. Nuptiae clam instituuntur. *Flores oculis nostris nudis vix conspiciuntur.* CRYPTOGAMIA." The "Nuptiae Publicae," which Linnaeus by an oversight failed to designate as PHANEROGAMIA, are once more broken down into two, as follows: "Monoclinia. Mariti & Uxores uno eodemque Thalamo gaudent. *Flores omnes hermaphroditi sunt, & stamina cum pistillis in eodem flore,*" "Diclinia. a δὶς bis & κλίνη Lectus, Thalamus. Mariti seu feminae distinctis thalamis gaudent, *Flores masculini vel feminini in eadem specie.*"

Thus robustly begun, this key continues in the same vein assimilating the stamens to husbands and the pistils to wives, until "Syngenesia" is reached, in which "Mariti cum genitalibus foedus constituerunt," and "Polyandria" briefly described as a condition under which "Mariti viginta & ultra in eodem cum femina thalamo."

That such a key as this had an instantaneous and enormous appeal to the mind of the public can readily be understood. By a bold stroke of the pen the nebulous world of plants was made to act like husbands and wives in unconcerned freedom, and everybody prepared to grasp the meaning of Monoecia and Dioecia, Syngenesia and Polygamia without effort. The educational value of this key, scientifically speaking, was tremendous, for it dispensed with musty tomes, learned verbiage, pompous trappings, and the like, to appeal directly to the flowers of the field. Very few works may compete with the *Systema Naturae* in purposefulness and power of well-meant vulgarization.

The boldness of the Linnean stroke raised in some quarters an outcry that this wild man was a crackpot. Siegesbeck, for instance, who could not see that the genius and the crackpot can look alike, but only the former yields true service, came forward with an account of "Botanosophiae verioris," dignified and orthodox botany, as we might say, in which he proclaimed that God could not permit, even among plants, "Such odious vice as that several males (anthers) should possess one wife (pistil) in common, or that a true husband should, in certain composite flowers, besides its legitimate partner, have near it illegitimate mistresses" (B. D. Jackson, *Linnaeus,* 170. 1923).

At this late hour, we are fortunately free from the necessity of sitting as judge on the petty morals of the case, and quite aware that Linnaeus' thunderbolt aroused a niggardly world to pay salaries even to some in the Siegesbeckian tradition. The question which is relevant to us is: Did Linnaeus thoroughly accept the Sexual System? The apparent answer should be yes, for this System is associated with his name wherever botany is taught, and is definitely used in the Linnean works. The System is glaringly artificial, for it associates, for instance, *Asarum, Portulaca,* and *Triumfetta* in one group. If Linnaeus accepted it without qualification, he is not to be rated

as a modern botanist, despite his having given us the binomial system of nomenclature.

The years spent by Linnaeus in western Europe (April 1735 to June 1738) are crucial for botany. Linnaeus published in this period much which he had prepared, if not actually written, during his years as an impecunious and often harassed student at the University of Uppsala. Nothing, however, is immature or half-baked in these works; Linnaeus comes out of their pages like Minerva out of the brains of Jupiter, armed and clad from head to foot. Unknown as they are today to the botanical majority, these works rank as Linnaeus's very best, and whatever he later achieved, when possessed of vastly greater means, can be traced directly to them.

Here are some of the thoughts of Linnaeus, clearly expressed in the three years which followed the publication of the Systema Naturae in 1735:

(a) Nothing can be understood without a clear method by which things like and unlike can be set apart. Our concepts are bound to be much clearer if we use as natural a method as possible. A natural method is all the more necessary, and all the more hard to write, as we face a greater number of subjects. Since by the Creator's fiat the world of plants is all-pervading, it is in botany that a natural method has the best chance of being ultimately worked out. Only through this method may we hope to gain a lucid perception of plant-life.[2]

(b) Many are preyed upon by an almost morbid fear of using some method of classification to which they are not accustomed. Some would rather read the most elementary primer than to consult a work which does not suit their notions. Since it is probable that most botanists establish their preferences in their early years, the students should be accustomed to use all kinds of methods, thereby freeing their minds from pettiness. Even a student is qualified to work out a system of his own if he does not find what he looks for in the current systems. For the same genera are not known to every botanist.[3]

The texts quoted are a sample of the Linnean thought, and could be freely implemented if space did not forbid. To comment on them is superfluous. Linnaeus definitely knew that classification is ultimately bound to rest

[2] *Genera Plantarum*, Ratio Operis. No. 1. 1737. "Omnia, quae a nobis vere dignosci possunt, dependent a clara Methodo, qua distinguimus similia a dissimilibus. Haec Methodus quo magis naturales comprehendit distinctiones, eo clarior rerum nobis nascitur idaea. Quo circa plures versatur noster conceptus objecta, eo difficilius elaboratur methodus, ac magis necessaria evadit. Nullibi tot objecta humanis sensibus objecit Summus Conditor, ac in Regno Vegetabili, quod totum istum, quem inhabitamus, globum tegit, replet. Ergo si ullibi pura methodus e re est, sane hic; si Vegetabilium claram idaeam obtinere sperabimus."

[3] *Classes Plantarum*, Praefatio. 1738 "Nescio quid fascinat homines, ut non possint alteram methodum videre absque perturbatione; potius legunt libellum secundum A.B.C. scriptum, quam secundum notas aliquas plantae; credo vix aliud, quam Botanici ad unam methodum dispositus a teneris animus; optandum itaque foret, tyrones omnibus ut assuescerent methodis, ut nugae istae semel evanescerent . . . Possunt & Tyrones, si planta in uno alterove systemate non reperiant, mox tertium quartumve evolvere; non enim omnibus Botanicis eadem nota fuere genera."

upon broad evolutive concepts, the presence of connecting links among plants being a gift of Flora to her tired adepts. His mind was early steeped in realities rather than wrapped up in scraps of paper. Had he witnessed the efforts of gentlemen to decide whether an apple is "branch" or "leaf," he would have eaten the apple, I fancy, then asked: "Well, boys, am I digesting a twig or a leaf?"

We have so thoroughly schooled ourselves into believing that Linnaeus is the father of the Dodecandria Trigynia and like amenities that we are seldom aware that he evolved not one, but three systems of classification: (a) the Sexual System, with which his name is unfortunately associated in the mind of most; (b) the Calycinal Method, arranged very much in the manner of the classification of Tournefort; (c) the so-called Fragmenta Methodi Naturalis, which are a lasting monument to the Linnean thought.

These three systems are compared and appraised in the pages of the *Classes Plantarum* (1738) as follows:

(a) *Sexual System.* The inadequacy of this system cannot be denied, and is freely acknowledged. It includes as many natural classes and orders as any other system, although exact parallels in this respect may hardly be drawn. Neither this system nor any other may lay claim to being natural.[4]

(b) *Calycinal Method.* The acknowledged purpose of this method is that of giving easy definitions of the calyx [flower] in all its aspects, different arrangements, and characters, this to familiarize beginners in botany with the proper dissection of the floral organs.[5]

(c) *Fragments of the Natural Method.* A truly natural method is the highest goal of systematic botany. Ill-informed botanists believe that such a method has little value, but well-informed ones know that the contrary is true. No one has so far succeeded in designing a true natural method. I [Linnaeus] have labored long trying to work out such a method, and done all I could, without reaching my aim. I will work at this task my whole life, publishing what I shall discover. He to whom it will be granted to perfect a natural method will rank as high as the God Apollo. It is impossible to give a key of the natural method before having placed every plant correctly as to order. It is not enough to define an order using the common characters of its genera, but data must be provided in addition by which one order can be set aside from another. My work is restricted to orders [i.e., families in the modern sense] because once these are correctly placed, the classes [i.e., orders in the modern sense] can be worked out at ease. No a priori rules can be laid down to write a natural method, and no part of the flower and fruit comes first in the sequence of the characters to be used. All that may count

[4] Op. cit. 440. "Classes vel ordines naturales admisit tot, quot ulla methodus alia, numerus tamen genio ubique fruitur suo; obstacula quae methodo contraria erant collegi, candidus imperti; Naturalem methodum nec hanc, nec aliam vocaverim ullam."

[5] Op. cit. 404. "Volui itaque in Tyronum gratiam methodum aliam plane proponere, inque ea Calycis species, differentias, proprietatesque facile omnes primarias describere, uti facilius adsuescerent Calycum dissectionibus Juniores Botanici."

toward such a method is the symmetry of every part, which is often peculiar to each group. Those who endeavor to provide a key to the natural method will be well advised if they pay close attention to the position of the seed in particular. Let everybody correct, extend, and perfect this method who can. Let those leave it alone who cannot. Those who can are the best of botanists.[6]

It is clear from these quotations (many others indeed could be given to the same effect), that Linnaeus had a low opinion both of the calycinal method and of the sexual system; witness the fact that he never used them to instruct the best of his students (see Ventenat, Tabl. Règ. Vég. **1**: xvii. 1799; Jackson, op. cit. 364). His preferences wholly went to the natural method. The high level of systematic thinking which permeates the "Fragmenta Methodi Naturalis" in the *Classes Plantarum* (1738) is transparent at a glance through its pages. Order I includes *Arum*, *Dracontium*, *Calla*, *Acorus*, *Saururus*, and *Piper*, possible additions being suggested in certain genera, as yet ill known from the works of Plumier and Rheede. Order XXVI covers *Theobroma*, *Corchorus*, *Heliocarpus*, *Triumfetta*, *Bixa*, *Clusia*, *Kiggelaria*, *Grewia*, *Tilia*, *Muntingia*, and *Sloanea*, which bears witness to a keen sense of broad affinities. Order XLVII accommodates the Euphorbiaceae with *Euphorbia*, *Dalechampia*, *Clutia*, *Osyris*, *Andrachne*, *Phyllanthus*, *Croton*, *Jatropha*, *Ricinus*, *Acalypha*, *Tragia*, *Mercurialis*, and *Cliffortia*, thus scoring high in a group in which true affinities are not easily detected. Order XX, with *Ficus*, *Dorstenia*, *Parietaria*, *Urtica*, and *Morus*, speaks for itself, considering that a fig and a nettle are not immediately seen to be closely related. Many other Orders can readily be recognized as the fair counterpart of modern families (granted that unwelcome additions are often not lacking) such as Order XXII (Araliaceae and Umbelliferae), Order XXIII (Ranunculaceae), Order XLIV (Rubiaceae). Even where Linnaeus fails, as in Order XIX, containing *Viburnum*, *Tinus*, *Opulus*, *Sambucus*, *Rondeletia*, *Bellonia*, *Cornus*, *Maurocenia*, *Cassine*, *Rhus*, *Celastrus*, *Evonymus*, he shows himself a keen student of floral symmetry and structure in the abstract.

[6] Op. cit. 484–487, Nos. 1, 4, 7, 8, 9, 11, 12, 13. "Primum & ultimum in parte Systematica Botanices quaesitum est Methodus Naturalis; Haec adeo a Botanicis minus doctis vili habita; a sapientioribus vero tanti semper aestimata, adhuc licet detecta nondum. . . . Diu & Ego circa methodum naturalem inveniendam laboravi, bene multa quae adderem obtinui, perficere non potui, continuaturus dum vixero; interim quae novi proponam: qui paucas, quae restant, bene absolvitur plantas, omnibus magnus erit Apollo. . . . *Clavis* methodi non dari potest antequam omnes plantae relatae sunt ad ordines. . . . Non satis est in definitione ordinis dedisse notas communes, nisi & his intersint, quae etiam eam ab omnibus aliis distinguant. . . . Classes nullas propono, sed solos ordines, detectis ordinibus, dein in classicis labor facilis erit. . . . Nulla hic valet regula a priori, nec una vel altera pars fructificationis, sed solum simplex symmetria omnium partium, quam notae saepe propriae indicant. . . . Qui Clavem fabricare student, sciant nullam partem universalem magis valere, quam illam a *situ*, praesertim *seminis*. . . . Emendent, augeant perficiant hanc methodum qui possunt: desistant qui impares sunt; qui valent, Botanici sunt Eximii."

Enough evidence is at hand to hail Linnaeus as the main founder of the natural method, that is, of true classification. Nor was his thought ill at ease upon the limits between artificial and natural classification, having reached the degree of maturity necessary to draw a sharp line *between description and interpretation.*[7] Linnaeus belongs to us, not to the past. The publication of the *Classes Plantarum* is a landmark of botany, and 1738 a memorable year in our annals.

If Linnaeus so clearly perceived the nature of things past and of things to come, freely admitting that every artificial system was bound to give way as soon as a natural system could be devised (Class. Plant., Praefatio. 1738), why did he not use this system in his works?

The mind of certain men is so ultimately gifted and so all-pervading that these men are inclined to see any important issue *sub specie aeternitatis*, as it were, making light of the present in anticipation of the future. Linnaeus had probed the difficulties inherent in a natural method, and come to the ultimate conclusion that such a method could not be brought into flower until the tides of time should return over and over again to the same shores. How correct he was we know, who still feel that a natural system is not wholly within our grasp. Other men, not less gifted and perhaps not less profound, cater to the present, feeling that every day is sufficient unto itself, and that to the individual *mors est ultima linea rerum*. To decide between these two philosophies, and to judge of the ultimate greatness of all these men is not easy, although many, among them myself, are ready to hail active imperfections in preference to ever deferred perfection. All we may say is that, broadly speaking, Linnaeus could probably not put up with active imperfection, being great enough, however, to school others in its use and limitations.

As a teacher, Linnaeus, moreover, must have felt, like another competent teacher, Amos Eaton, that the Sexual System had temporary value *as an artificial key*. Quoth Eaton (Man. Bot. North Am. ed. 6. **1**: 13. 1833): "The object of the Artificial system is merely to furnish a method for ascertaining the name of a plant. The object of the Natural system is to bring together into small groups, plants which resemble each other in their botanical affinities, sensible qualities and medicinal properties. The Artificial sys-

[7] Little less mature, if indeed at all, was the Linnean thought of 1737 on the limits between description and pure nomenclature. In his condemnation of redundant descriptive polynomials (Crit. Bot. 152. 1737; Phil. Bot. 204. 1751) Linnaeus laid down principles which, somewhat more stringently applied, had as their result the adoption of binomial nomenclature in 1753. The advantage of adopting binomials or short polynomials had not gone undetected, witness the catalogue of the Botanical Garden of Bologna, Italy (*Hortus Studiosorum Bononiae Consitus*), prepared and published by an obscure professor of botany, Ambrosino, in 1657. Linnaeus is the genius, however, to whom it was given to think himself out on principles before advancing concrete solutions. This lucidity of thought is the secret of his hold upon generations of naturalists.

tem has been very aptly compared to the dictionary, and the Natural, to the grammar of a language." To this Eaton added (op. cit. **1**: viii. 1833): "The Natural Method should engage the attention of the student, after he has become acquainted with about 400 species of plants, by the aid of the Artificial Method."[8] Eaton's opinions closely agree with those of Jaume-St. Hilaire (Pl. France **1**: xxiii–xxvii. 1805), written a full quarter of a century before. That Linnaeus meant the Sexual System as an artificial key can readily be seen. In the *Classes Plantarum* (1738) *Ficus* is properly entered in Order XX of the "Fragmenta Methodi Naturalis" (op. cit. 494), together with *Dorstenia*, *Parietaria*, *Urtica* and *Morus*, as we have seen. In the Systema Sexuale exhibited in the same work (op. cit. 483) *Ficus* is set out precisely where a beginner, not a botanist, would look for it, in the *Cryptogamia*, alone under *Plantae*. In the Methodus Sexualis (1737), appended to the *Genera Plantarum*, the same genus is freely shifted among different Classes and/or Orders if its sexual characters warrant it. Accordingly, *Rhamnus*, which in the *Classes Plantarum* (1738), is firmly kept under Pentandria Monogynia, is tossed about in the *Methodus Sexualis* (1737), as Pentandria Monogynia (its main position) Pentandria Trigynia, Dioecia Tetrandria, and Polygamia Dioecia. Since examples of this nature could be multiplied, nothing should be easier than to prove that Linnaeus was "inconsistent" in his handling of the Sexual System, and could hardly draw the line between a toadstool and a fig. Such a "proof," however, would merely show that its author knows nothing, convincing as the "proof" might be in point of fact.

Against Linnaeus and all his predecessors Adanson had a thesis to establish. The thesis was that all artificial methods were worthless, and that only the natural method could be used. Like Robert Brown, Adanson had travelled in the tropics, and there realized that the classifications of Tournefort,

[8] Eaton happens to be the author of a Natural Method of his own. Incensed by De Candolle's and Lindley's treatment of Jussieu as an "ordinary fellow laborer" (op. cit. **1**: iv), and believing that the aim of these systematists was "the total annihilation of the system of Jussieu" (op. cit. **2**: 3), Eaton reinstated the old Jussieuan names. He still called them orders, but used them sometimes as we do families. The outcome of Eaton's concern with justice and priority is baffling, to say the least. He divided, for instance, the "ORDER L. *Rhododendra*. LI. *Ericae*" into three groups of undefined rank, Ericeae, Vaccineae, and Pyrolaceae, subdividing the former into Ericeae verae and Rhodoraceae. The Order Berberides (op. cit. **2**: 104) he subdivided into Berbericleae and Hamamelideae, the Order Magnoliae (l.c.) into Magnoliaceae and Wintereae. His treatment of the magnoliaceous group is factually the same as that of De Candolle (in DC. Prodr. **1**: 77–79. 1824), who published the Magnoliaceae as a family (*Ordo* of De Candolle) with two tribes, Illicieae and Magnolieae. Contrariwise, the Berberides, as understood by Eaton, are meant as an order in the modern manner, that is, as a group of presumably allied families. Eaton proved unable to extricate priority from systematic concepts, but his concern with the units above the family, and his insistence upon older names, are not lacking in a constructive side. Bartling had at long last carefully described these units only three years before (1830), and Lindley was still to write about them three years later (1836). Eaton's Method seems to have been overlooked by nearly all indexers.

Linnaeus, and others were hopeless in the face of new aspects of nature. From his travels, and by lifelong study, he had reached the conclusion that plant distribution spoke a definite language to the systematist, and that the very concepts of the units used in classification should be redefined. This, and much else which space forbids me to mention, Adanson plainly states in his monumental preface to *Les Familles des Plantes* (**1**: clvi, clxvii, *et passim.* 1763), a work of lasting erudition, if not of dispassionate judgment. Unlike Linnaeus, Adanson had the soul of a philosopher inclined to take immediate action. As a clever polemist, but not as an unbiased critic, he dismissed everything which Linnaeus had done as too artificial or inconsequent (op. cit. **1**: xlii, xliii, xliv, xlvii), lumping together beyond the claims of justice as of one cloth the sexual system, the calycinal method, and the fragments of the natural method. That Adanson, enriched by his experiences as an explorer and as a thinker, had to broadcast his message in the face of sloth or actual opposition may induce us to forgive the poisonous sting of some of his comments, his boast that only three of his sixty-eight families, *Vaccinia*, *Cisti* and *Ara* (op. cit. **1**: cxcix) were not satisfactory, his lavish incorporation of doubtful or ill-known genera, and his flagrant breaches of good taste in priority.

Strange to say, the thought of Adanson had much in common with that of Linnaeus. Both these masters worshipped the natural method, and each gave us the outline of one. Both felt the need of artificial systems, or keys, of which Linnaeus gave us two, and Adanson sixty-five (op. cit. **1**: cccxi–cccxii). Both were hampered by lack of material and lack of knowledge. Coldly appraised by a systematist, the "familles" which so much pleased Adanson are readily seen not to be much better than the "fragmenta" which Adanson despised; witness, for instance, the content of the Tithymali of Adanson (op. cit. **2**: 354–358), and that of the Order XLVII of the *Classes Plantarum* of Linnaeus, later to become with some unwelcome additions the Tricocca of the *Philosophia Botanica* (32. 1751).[9] Considering the level at-

[9] The name Tricoccae (or Tricocca), together with several others which appear in the Linnean "Fragmenta Methodi Naturalis," is taken from Van Royen's *Florae Leydensis Prodromus* (1740), with or without very slight changes in the endings. A glance at the twenty Classes of Van Royen will readily convince a critical reader that Linnaeus owes little to him beyond occasional nomenclature. Van Royen had an understanding of natural classification, which the preface in his work reveals, but, very much like Ray, fell into error, carefully pointed out by Linnaeus, to attempt to define the Class (modern order) before the Order (modern family). The result is that the Aggregatae of Van Royen include under two subdivisions, Monopetalae and Pentapetalae, such genera as *Protea*, *Conocarpus*, *Cephalanthus*, *Morinda*, *Dipsacus*, *Scabiosa*, *Knautia*, *Dorstenia*, *Globularia*, *Lagoecia*, *Jasione*, *Brunia* and *Statice*. The Incompletae of Van Royen are a fantastic mixture of *Salicornia*, *Empetrum*, *Dodonaea*, *Hippophae*, *Celtis*, *Potamogeton*, *Chara*, *Thesium*, *Hedera*, *Ruscus*, *Alchemilla*, *Hura*, and the like. Certain of the Classes of Van Royen are much better than others, some, like the Tricoccae, almost natural. However, it is not so much the casual right or wrong guessing that stamps the true systematist, as the quality of his thought *as a whole*. As a thinker, Van Royen does not begin to compare with Linnaeus, and is below Adanson, Lamarck, and A. L. de Jussieu.

tained by botany in 1738 and 1763, it is not surprising that Linnaeus and Adanson should break about even in systematic performance. To Adanson credit must be due, however, in several respects: (1) By his uncompromising rejection of the very principles of artificial classification, Adanson focussed the attention of the botanical world upon the need of proceeding with natural classification in a positive rather than in an abstract manner. To this extent, Adanson had most likely a powerful influence upon Bernard and Antoine Laurent de Jussieu, the Apollo of the natural method.[10] (2) Adanson provided description of groups more or less akin to modern families or orders, and of their major subdivisions, whereas Linnaeus had written only series of generic names under undescribed orders. (3) Lastly, Adanson soared to a perception of the vastness and complexity of the kingdom of plants, from this deriving conclusions of value to the botanist in various fields. Perhaps too little credit has been given him in this respect. Hasty perusers of the *Familles des Plantes*, repelled by a unique spelling of Adansonian concoction and untold barbarous generic names, all too readily conclude that Adanson is a crackpot. Such a conclusion is absolutely erroneous, for Adanson soars high among the masters of botany. So much could easily be proved, if space did not forbid my delving further into Adansonian thought here.

The ground had been thoroughly laid by Linnaeus and Adanson to use natural classification in 1763, but the joint significance of the work of the two masters seems to have been lost on their immediate contemporaries. Bernard de Jussieu, their most receptive listener, published nothing of botanical significance, leaving it to his nephew Antoine Laurent to pick up the good trail about a quarter of a century later. Five years after the publication of Adanson's *Familles*, and Linnaeus's second edition of the *Philosophia Botanica*, Haller released his *Historia Stirpium Indigenarum Helvetiae* (1768), a work which contains (**1**: xxv–lviii) a laborious superb bibliography. Haller comments (op. cit. xxii) that he could have saved himself a great deal of labor had he chosen to follow the Linnean classification, meaning by this the sexual system. However, Haller confides, this was too much for him to do, considering that Linnaeus had torn to shreds even the most natural groups, as the *Gramineae*. So as not to follow Linnaeus, Haller drew

[10] Strong evidence is at hand that Adanson might have had more than influence upon Bernard and Antoine Laurent de Jussieu. The seldom read second edition of the *Familles des Plantes*, edited by Alexander Adanson & Payer, contains a parenthetic statement (**1**: 134. 1847), evidently culled from Adanson's original manuscript, in which the latter affirms that the outline of the *Familles*, sent with full details to Bernard de Jussieu in 1750 from West Africa, had never been returned, either by Bernard or by Antoine Laurent. This statement does not appear in the original edition (op. cit. **1**: cc), which is good evidence of Adanson's love of truth rather than quarrels. On points involving fact, and even more tendencies, Adanson was outspoken, occasionally rash. On matters of precedence and personal satisfaction he could hold his peace.

up his own "Systema," hoping thereby to keep intact as many natural groups as possible. Since this "Systema" is artificial, Haller was fated to fail in his attempt at building natural groups. His key (Tabula Classium et Generum) is by no means easy to handle; one of the groups under Classis I, which includes the Compositae, is made of the genera *Senecio, Solidago, Aster, Erigeron, Doronicum,* and *Arnica.* Had Haller turned to Adanson's *Familles* he would have found therein "Famille XVI. Les Composées. *Compositae,*" a close match of Linnaeus' "Compositi" (Phil. Bot. ed. 2. 33. 1763). His group Haller would have found, moreover, fairly well represented by Adanson's "VIII. Section. Les Jacobées. *Jacobeae*" (op. cit. **2**: 123), and included under Linnaeus "*Compositi Corymbiferi*" (loc. cit.). Using any of these names with some emendation, Haller could have saved himself the trouble of erecting a new "Systema," and given partial keys to his satisfaction. In fairness to Haller, it must be said that the botanists of the day could not think this simple way, and that the efforts of Linnaeus and Adanson were still gems in the rough. So much, however, does not detract from the fact that natural classification was already alive in 1763, and that a creative mind could with little effort free himself by then of the stifling belief that describing rather than understanding is the soul of science.

Gleditsch's *Systema Plantarum a Staminum Situ* (1764), is characteristic of a form of thought for which the Linnean Fragmenta Methodi Naturalis of 1738 did not exist. New terms are used in this "Systema," the Phaenostemonis replacing the Phanerogamia, and the Cryptostemonis the Cryptogamia, but, as one would expect, the old wine still fills the old skins. *Cactus,* as manipulated by Gleditsch (op. cit. 274), aligns itself with *Mesembryanthemum, Eugenia, Philadelphus, Psidium, Myrtus, Punica, Crataegus, Sorbus, Mespilus,* and *Pyrus;* and *Euphorbia,* enthroned in the *Thalamostemones Dodecantherae,* is satisfied to rest (op. cit. 105–107) with *Rhizophora, Garcinia, Crataeva, Triumfetta, Peganum, Nitraria, Portulaca, Heliocarpus, Reseda, Menispermum, Illicium,* and *Sempervivum.* With this, everything is back at least to the early days of Tournefort.

LAMARCK, A. L. DE JUSSIEU, VENTENAT and NECKER

The *Flore Françoise* published by Lamarck in 1778 is striking in being written throughout as an artificial key. The preface of this work is remarkable. In it, an artificial key is represented as something wholly unlike true classification. The thought is not new, as we know, following as it does Linnean lines of 1738. However, unlike Linnaeus, Lamarck draws rigorous, practical conclusions. He points out (op. cit. **1**: lix) that an artificial method, or key, can have no other purpose than yielding the name of a plant already described. The basic principles for the making of a good key, Lamarck states, are two: (a) every character must be made use of, so far as possible, with the

exception of those which are not readily apparent; (b) the descriptions in the key must be clean-cut, and the key-groups sharply defined. Lamarck comments upon the second principle (op. cit. **1**: lx–lxi) characteristically as follows: Since it is patent that the key-groups are bound to violate somewhere even the sharpest natural affinities, we must set our minds at rest, accepting the fact that these affinities will be disregarded as a matter of course. Nothing else counts for so much as a method of keying which establishes hard and fast groups, and leads to describing them in an unequivocal manner. It is immaterial that these groups cut through natural affinities.[11] Fully as lucid are the principles which Lamarck lays down to write botany along natural lines. These principles (op. cit. **1**: xcii) are (a) to determine which plant is to come first, as initial in a natural series; (b) to provide rules whereby the species can best be brought together; (c) to lay down a consistent line of treatment for orders and families which cannot be broken into lesser units. Lamarck concludes in what is to us a strange vein (op. cit. **1**: cxviii), saying that so poor is the flora of France that it can best be treated only under the artificial method, that is, by a key. Naturally treated, Lamarck argues, the flora of France would be riddled with gaps.

To us, who are thoroughly aware of the essential difference between a key and classification, Lamarck's comments sound anything but revolutionary. To Haller, to Gleditsch, and to the multitude who still strove to mix description and interpretation, concocting artificial keys that should be factual classification, Lamarck's warnings were thunderbolts. That which Ray had felt Linnaeus passionately preached in low tones, Adanson stated in a rasping voice, and Haller and Gleditsch never understood, Lamarck laid down in a masterly hand as common sense, which of all human weapons is the most powerful in the long run. Wholly to the point, if beyond the truth of history, A. P. De Candolle hailed the *Flore Françoise* (Fl. Franç. ed. 3 **1**: vii. 1805) as the first work in which the soul of the natural and artificial method had been laid bare. Linnaeus in his *Classes Plantarum* had indeed been first to see clearly the light, but Lamarck had been second to none in carrying this light to its ultimate limits. Lamarck thoroughly uproots the hoary confusion between description and interpretation, between mere key making and genuine systematic thinking. Unknown to most, the year 1778 looms large in the annals of botanical thought.

In the *Genera Plantarum* (1789) of Antoine Laurent de Jussieu description and interpretation are kept apart in the best Lamarckian style. Jussieu recognizes a hundred "Ordines Naturales," more or less agreeing with

[11] "Ayant reconnu qu'on ne peut faire une seule division qui ne rompe quelque part des rapports très-marqués, on doit se mettre parfaitement à son aise sur cet objet, s'occuper uniquement de la sûreté de la methode, former des divisions tranchantes & circonscrites par des définitions à l'abri de toute équivoque, sans avoir égard aux séparations frappantes que ces divisions peuvent occasioner."

families in the modern sense, and fifteen "Classes." The classes are keyed out in one page (op. cit. lxxi), the key resting upon a division of plants into Acotyledones, Monocotyledones, and Dicotyledones, and lesser groups based upon peculiarities of the corolla and the stamens. The orders are dealt with at length, but not keyed. The sharp eye of Antoine Laurent realized, no doubt, that some classes were natural, like No. XII, including Araliaceae and Umbelliferae, while others were not, like No. XV, associating the Euphorbiaceae with the Cucurbitaceae, Urticaceae, Amentaceae, and Coniferae. However, the classes bore no name, and were non-committal, as we now say, hardly better than artificial or occasionally natural key-groups. Altogether different was the case with the Orders, which Jussieu strove to maintain natural throughout. In the *Flore Françoise* Lamarck had chosen to abide by a key, without using natural classification; in the *Genera Plantarum*, Jussieu used both a key and natural classification. In this Jussieu consciously set a precedent, a far-reaching one, considering the fundamental nature of the *Genera*, and its immediate acceptance by the best botanical minds of the time.

Behind Lamarck and Antoine Laurent de Jussieu, looms large the silent figure of Bernard de Jussieu. While Adanson was busily writing, and Linnaeus in part theorizing, Bernard acted in the most direct and unpretentious manner. As Antoine Laurent tells us (op. cit. xxxvi, xlix, lxiii–lxx), Bernard in 1759 laid out the plants of the royal garden at the Trianon according to the natural system. Later on, in 1774, the same plan was introduced in the botanical garden of Paris, and on this the *Genera* was patterned. The natural system of Bernard de Jussieu closely followed the lines of Linnaeus's Fragmenta Methodi Naturalis, and Adanson's *Familles des Plantes*, which can readily be seen by comparing, for instance, the *Sempervivae* of Bernard (op. cit. lxix) with the *Succulentae* of Linnaeus (Phil. Bot. ed. 2. 36. 1763) and the *Portulacae* of Adanson (Fam. Pl. **2**: 235. 1763).

Bernard's quiet deed powerfully influenced botanical thought. Linnaeus's bold stroke had popularized the study of botany in 1735 by introducing the sexual system, and Bernard's arrangement in 1759 made it possible for every thinking botanist to see the natural method of classification at work. Such a person could leisurely walk through the alleys of the Trianon, and of the botanical garden of Paris, think his own thoughts, leave, and return. Since thought feeds on observation, and ideas come at leisure, mostly to those who choose to live with plants rather than to finger them only in an herbarium, Bernard's exhibits gave to everybody who cared to listen a lecture of the most objective and cogent sort. As new plants came in, from distant or from near lands, it was natural that they should be fitted into the frames of the natural system, for this system every French botanist had in mind. As the pieces of a puzzle are sorted and shifted, so were new plants set under this or that order and group, each increase in knowledge making it

easier to deepen and to elaborate the system. It was known within thirty years that the Succulentae of Bernard actually fell into six natural groups, which Antoine Laurent published as the Succulentae, *sensu stricto*, the Saxifrageae, the Cacti, the Portulacae, and the Ficoideae. Others could theorize about these groups in Germany, Italy, or England; in France *they had seen them*. The objective method of dealing with vegetables inaugurated in Paris insured the preeminence of French systematic thought at a critical moment in the history of botany. Could we follow a like method, creating a center of botanical endeavor where plants can easily be grown, and be thought upon as they grow, we would insure, no doubt, felicitous results, for neither nature nor man does change.

Adanson had the manuscript of the *Familles des Plantes* available in 1759, and the fact that Bernard de Jussieu laid out the plants of the Trianon in a natural manner the very same year may not be a coincidence, as we have seen. Through the *Classes Plantarum* (1738) the *Familles des Plantes* (1763) and the *Genera Plantarum* (1789) runs the same thread. Bernard de Jussieu published nothing which a botanist is supposed to know about, but without him Antoine Laurent could hardly have written the epochal *Genera Plantarum*.

The thought of Necker has weighed heavily upon many consciences, my own not excluded (Croizat & Hara in Jour. Jap. Bot. **16**: 384. 1940). Yet, when it is seen as part of a larger whole, this thought yields up most of its mysteries. Here was a man of prodigious industry but confused thinking, for whom neither Linnaeus nor Adanson had ever written a creative word. His *Elementa Botanica* (1790) is unadulterated artificial classification to be used as a key (op. cit. **1**: xvi–xvii *et passim*). Like every uncreative mind, Necker felt the greatest need for new words, to take the place of new thoughts. Accordingly, Linnaeus' Compositi and Adanson's Compositae would not do, but the "Genus" Actinophytum had to be coined instead. Aware of the artificiality of the Linnean Sexual System, but conscious, as it seems, that the Linnean genus was a tolerably natural group, he decided to call "genera" units above the commonly accepted genera, which units he thought, mayhap, to be natural.[12] Under these he set out the "Species

[12] This notion may not even be original with Necker. Ray had spoken (Meth. Pl. Emen. Praecognoscenda. 1703) of "Genera summa . . . subalterna & infima," and designated his main units as "Genera." In 1737 Linnaeus had admitted (Crit. Bot. 138. 1737) that the class (modern order) could be understood as "Genus summum," and the order (modern family) as "Genus intermedium." As if sensing the danger that this admission could be misunderstood and abused, Linnaeus carefully reworded it in the *Philosophia Botanica* (136. 1751), as follows: "Quod valet de charactere generico, valet etiam de classico, licet in hoc latius sumantur omnia. Generum genus est Ordo, ordinum autem genus Classis est." This revision might have come too late; it is likely that Necker decided that the "Genus intermedium" could be deprived of its qualifying adjective, and left as Genus, a tail in the shape of the adjective Naturalis or Immortalis being affixed meanwhile to the Species. Some souls cannot withstand temptations of this sort.

Naturalis" or "Species Immortalis," which by being a group of related species could be little else but a genus in the Linnean sense. The "Prolis" was the individual plant. The results of these manipulations are dismaying, and it seem altogether likely that Necker himself, having been formed as a botanist in the Linnean school, could never fully eject from his subconscious the Linnean units, while mixing them up with his novelties. One who does not well know what he wishes to say may always be quoted in any way a commentator likes, and Necker may be presented, perhaps, both as a genius and as a crackpot by parties willing to make convenient abstracts from his lucubrations. The fact that he can be made to play both roles, while certainly yielding nothing creative, shows Necker to belong with the crackpots rather than with the geniuses. If we turn to his *Elementa*, (**3**: 102–122. 1790) we find, for instance, the "genus" Daphonophytum which includes *Ceratocarpus*, *Cynomorium*, *Gunnera*, *Antidesma* (*Stilago*), *Hura*, *Salacia*, *Nepenthes*, *Aristolochia*, *Osyris*, *Eleagnus*, *Gouania*, *Bucida*, *Waldschmidtia*, *Conocarpus*, *Saraca*, *Pistia*, *Cytinus*, *Asarum*, *Tamus*, *Rajania*, *Hippophae*, *Theligonum*, *Viscum*, *Datisca*, *Terminalia*, *Nyssa*, *Stratiotes*, *Montinia*, *Casuarina*, and *Aegopricon*. This list speaks for itself, and if Necker happens to concoct a "genus" which is natural it is certainly Nature's fault. Since Necker was fond of small units, in the "Species Naturales" he set out, no doubt, "species" of the kind which contain the ghost of a good genus. His *Aroton* may well be *Caperonia*, his *Cratochwilia* is perhaps *Bridelia*, his *Arachne* is *Sauropus*, his *Athymalus* is the segregate of *Euphorbia* which Haworth later called *Dactylanthes*. All these "species" have priority in the Euphorbiaceae, but, to forget the safety valve offered an harassed taxonomist by the *nomina generica conservanda*, the plain truth is that these names are illegitimate, because they subvert the prescribed sequence of the units of classification. If we honor these "species," we might as well honor "genus" Daphonophytum, typifying it through allegories and fictions. A simpler solution is that those who formally leave the botanical fold be kept out of it, if this happens to be legal. The matter is not offered here for immediate discussion, because only the value of Necker's systematic thought is in question. On the score of this value few indeed will be found to disagree.

TRIMMING AND POLISHING

With the publication of de Jussieu's *Genera* in 1789 the period lasting from 1738 to 1790 comes to an end, in which true classification extricates itself from the thraldom of key-making, and interpretive systematic botany triumphs, in principle, over descriptive taxonomy. The period that opens in 1790 is essentially concerned with three phases of endeavor: (a) defining the units above the family; (b) defining the units between the family and the genus; (c) providing a suitable nomenclature for these units.

Of these three undertakings the first was fated to come to the fore later than the two others. So long as the affinities between families were poorly understood, few indeed would worry about the concepts and the names which might apply to the order and to the class. To determine the fate of the units between the family and the genus was more urgent, and it was not less urgent to name properly the families and their subordinate units.

Linnaeus had adopted special names for his "Fragmenta" in the first edition of the *Philosophia Botanica* (1751) such as Vepreculae, Scabridae, Cucurbitaceae, Tricoccae, also retaining traditional designations like Palmae, Coniferae, Compositi, and the like. Adanson preferred to use almost exclusively the plural of some characteristic generic name, turning the French vernacular designations "les cistes," "les airèles," "les pourpiers," for instance, into their pure Latin equivalents, Cisti, Vaccinia, and Portulacae. Unlike Linnaeus', Adanson's nomenclature was marred by ambiguity, for "les cistes," *Cisti*, could be understood to mean certain species of *Cistus*, or the group, or family, which Adanson had erected around *Cistus*.

Between 1763 and 1825, the French had a factual monopoly of natural classification, and certain aspects of the nomenclature of the family cannot be understood unless account is taken of French linguistic peculiarities and uses. To us, terms like the Cactaceae, the Euphorbiaceae, the Taxaceae are part and parcel of the *English* botanical tongue, for we have no vernacular equivalent with which to replace them. Not so with the French, who would refer to the "Cactées," "Euphorbiacées," and "Taxacées" as a matter of course, and use the Latin forms of these names only in strictly formal work. In creating names for families and like units, the French coined as a rule the French term first, later translating it into Latin. The result of this linguistic quirk was that, in all too many cases, French euphony prevailed in the matter of name-giving. It is not clear to us, for instance, why Jaume-St. Hilaire should have rejected the name Onagrae of Adanson and Jussieu (Expos. Fam. Nat. **2**: 148. 1805) in favor of a new Onagrariae. The only possible explanation for this departure from accepted endings is that "Onagraires" is more agreeable to a French ear than "Onagrées" or "Onagracées." Even an ill-sounding name is acceptable when it has been in constant use, but French authors between 1789 and 1825 were coining *new* names, and with them euphony, even as individually understood, rated as no paltry consideration. Rules of nomenclature with binding power they had none. The elder De Candolle, for instance, gave a false reference to the "Magnoliacées Juss. gen. 280" and the "Annonacées Juss. 283" (Théor. Elém. Bot. ed. 1, 213. 1813) for the same reasons; Jussieu had published, in truth, the Magnoliae and the Anonae. The Code of Paris, of 1867, maintained the Ordo and the French term Famille as synonymous partly on these same grounds (Lois Nom. Bot. **1867**: 15; Comm. 34. 1867), which proved unfortunate.

The proper nomenclature of the family was dealt with by the elder De Candolle in his *Théorie Elémentaire de la Botanique* (247, 1813; ed. 2, 276–278. 1819). He accepted the ending *-aceae*, praised as good forms Liliaceae, Rosaceae, Anthirrineae, Ericineae, and Laurinae, disapproved of the endings in *-oideae*, and suggested that such names as Salicariae, Thymeleae, and Frangulacae should be used in certain cases. In 1819 (op. cit. 278) he advanced a nomenclatural innovation to forestall ambiguity between the name of a family and that of a tribe. The name of a family should be derived from the name of an important genus under it made longer by one syllable, witness Ranunculaceae, Myrtineae, Flacourtianae; that of a tribe merely by making an adjective as Ranunculeae, Myrteae, and Flacourtieae. It will readily be seen that these rules left euphony free play, although they tended to set up a factual standard for the publication of tribal names ending in *-eae*. Plural generic names could be tolerated only if they cause no ambiguity.

Antoine Laurent de Jussieu had given little thought to nomenclatural amenities. He had retained traditional names (Palmae, Coniferae, Cruciferae, etc.) together with plural generic designations in the Adansonian tradition (Asparagi, Asphodeli, Narcissi, etc.), names ending in *-aceae* (Campanulaceae, Rubiaceae, Papaveraceae, etc.), in *-eae* (Borragineae, Polygoneae, Jasmineae, etc.), in *-oideae* (Aroideae, Cyperoideae, etc.). Ventenat rejected much of this loose nomenclature (Tabl. Règn. Vég. 1799), intending to do away with generic plural names of Adansonian flavor, and to standardize the endings somewhat. Accordingly, he replaced the Pediculares of Jussieu with his own Orobanchoideae and Rhinanthoideae, the Euphorbiae with the Tithymaloideae, the Guaiacanae with the Ebenaceae, the Rhododendra with the Rhodoraceae, the Plantagines with the Plantagineae. Ventenat reinstated in addition certain ancient Linnean names, such as the Bicornes for Jussieu's Ericae, and himself introduced like names; witness the Hilospermae to replace Jussieu's Sapotae, the Glyptospermae instead of the Anonae.

Since neither A. P. De Candolle (Fl. Franç. ed. 3. 1805) nor Jaume-St. Hilaire (Exp. Fam. Nat. Pl. 1805[13]) liked endings in *-oideae*, they ruled out Ventenat's Tithymaloideae, replacing it with the Euphorbiaceae, and so on.

[13] These two important works were both published in 1805, "An XIII." Their priority is to be settled as follows: (1) *Jaume-St. Hilaire*. Actually published in *March, 1805* (See Intelligenzbl. Allg. Lit.-Zeitung **1805**: 427. 1805, offering the work for sale before April 3rd; Jour. Gén. Litt. France **1805**: 36. 1805). (2) *Lamarck & Decandolle*. Actually published in *September, 1805* (See Jour. Gén. Litt. France **1805**: 260. 1805). The publication was intended for the beginning of the year, but delayed by corrections (op. cit. 261). This may account for Labillardière's statement, dated July 8th, 1805 (in Ann. Mus. Hist. Nat. **6**: 451. 1805, XIII), carrying an implication that the work in question was by then already out of press. It may be added that the references here cited are a ready source of valuable data for the actual dates of publication of most works credited to this period.

We must come to the first volume of De Candolle's *Prodromus* (1824) to find a beginning of true standardization, with family names ending in *-aceae* (Ranunculaceae, Dilleniaceae, Magnoliaceae, Anonaceae, Podophyllaceae, etc.), in *-eae* (Berberideae, Capparideae, Flacourtianeae, Bixineae, etc.) together with some ancient designations like Cruciferae. The subdivisions of the family are tribes standardized mostly to end in *-eae* (Illicieae, Magnolieae, Lardizabaleae, Menispermeae, etc.). This is the nomenclature still followed, in the main, in Bentham & Hooker's *Genera Plantarum* half a century later.

The family, as we understand it, was mostly designated as Ordo, which was the old Linnean designation of the "Fragmenta." The unit below the Ordo was the Sectio, named or unnamed, in the works of Adanson, Ventenat, Jaume-St. Hilaire. However, De Candolle designated as Ordo as late as 1805 (Fl. Franç, ed. 3. **3**: 318, 321) the Sectio of other authors, publishing for instance the "famille" Urticeae with two "Ordines," Artocarpeae and Urticeae. In 1819, De Candolle had changed his mind, and used the rank Tribus for the same category.

In conclusion, when systematic botany began to leave France, the following had been achieved: (a) the "Subclassis" (equivalent to the current Suborder) had gained nomenclatural recognition with the Thalamiflorae, Calyciflorae, etc., of De Candolle; (b) the "Ordo," no longer a Tribe, but matching the current Family, had been standardized around endings in *-aceae* and *-eae*, some traditional names being retained throughout as the Cruciferae; (c) the "Tribus," embracing our own Subfamily and Tribe was firmly rooted in endings in *-eae*. We must come to Lindley, in the classic *Natural System of Botany* (1836[14]) to find a full standardization, the "Alliances" (modern Orders) ending in *-ales*, and the families in *-aceae*. This standardization, of course, was no more accepted by all than had been the nomenclature of De Candolle. The Code of Paris of 1867 left the field practically wide open. It stated that the families should end in *-aceae* (Art. 21), but authorized numerous exceptions on the ground of usage, legitimizing for instance (Art. 22) the Salicineae, the Berberideae, the Tamaricineae, the Dipterocarpeae, the Lentibularieae, in addition to the Compositae, the Labiatae and the like. The subfamilies ("subordines, subfamiliae") should end in *-eae* (Art. 23), the tribes and subtribes (Art. 24) in *-eae* or *-ineae*. The section dealing with the names above the genus is possibly the worst in the Code of Paris, attempting as it does to indorse almost every use and abuse under cover of long previous custom.

The omission from these pages of any reference to botanical thought in the United States is not accidental. As a matter of fact, the history of this

[14] This is the second edition. I have not been able to consult the first, which appears mostly to follow the Candollean classification.

thought is so interesting that justice may be done it only in the course of an extensive review. If Nuttall rates as an American, this country can readily be shown to have been not inferior to England in constructive systematic thinking between 1800 and 1830. Under the thin veneer of the Linnean Sexual System, which he fully rejected as early as 1825 (Jour. Acad. Nat. Sci. **5**: 132), Nuttall contributed in 1817 (op. cit. **1**: 111) searching discussions of natural affinities. In a work with the outward appearances of artificial classification, but as thoroughly imbued with Jussieuan spirit as Jussieu's own writings, Nuttall was the author of such groups as the Monotropeae (Gen. **1**: 272. 1818) and the Empetreae (Gen. **2**: 233), which were readily received by the progressive botanists of Europe. Nuttall's pedagogic work (Intr. Syst. Physiol. Bot. 1827) has a sweep and vigor of treatment which is not apparent in many of the writings of his contemporaries, and reveals him as a master of limpid thought and conscious purpose.

NOMENCLATURAL CONSIDERATIONS

The Rules of Vienna (1905), still in vigor in this respect, prescribe (Art. 23, Amsterdam Rules, 1935) that the name of a family must be derived from that of a present or former genus and must end in *-aceae*, allowing exceptions in favor of the traditional designations Palmae, Cruciferae, Compositae, and the like. Subfamilies (Art. 24) are to end in *-oideae*, tribes in *-eae*, and subtribes in *-inae*, all names to be derived from those of genera. The names above the family are left to a Recommendation (Rec. ix), advising that the Orders end in *-ales*, the Suborders being variously named, Tricoccae, for instance, but preferably ending in *-ineae*.

To analyze these Rules in detail is not the purpose of this study. I will point out here merely two cases which deserve immediate attention, and voice my opinion on their possible solution:

(a) A very great number of names with the above endings have been published by authors under ranks which make the endings untenable under the current Rules; witness Ventenat's Tithymaloideae announced as an order, but acceptable only as a subfamily; De Candolle's Artocarpeae published as an "Ordo" under a family, but with an ending legitimate for a tribe.

(b) Many names published by French authors in the French language have been latinized by later writers, witness the "Perideae" credited to Baillon by Pax & Hoffmann (in Engl. & Prantl, Nat. Pflanzenf. ed. 2, **19**(c): 153. 1931), whereas Baillon spoke of the "Péridées" (Ét. Gén. Euphorb. 433. 1858).

If we turn to authoritative literature for guidance, we find therein the most appalling confusion. German work, which is still our readiest source of reference for the nomenclature of units above the genus, can hardly be trusted. Engler & Krause (in Engl. & Prantl, Nat. Pflanzenf. ed. 2, **19**(c):

1. footn. 1931) comment on the Chailletaceae and the Dichapetalaceae in a manner which reveals total unfamiliarity with the rudiments of correct nomenclature, and shows that they are not aware that a family name may be conserved. Pax & Hoffmann (op. cit. 44) treat the Phyllantheae, a tribe of Bentham & Hooker, as an exact synonym of their own subfamily Phyllanthoideae, and maintain their own, and later, tribe Phyllantheae as legitimate. They, likewise, (op. cit. 89, 96) erect two subtribes, Regulares and Irregulares, under tribe Crozophoreae, in violation of the Rules concerning the proper ending for this category. Engler's Syllabus, ed. 8, 1919, accepts two subfamilies of Schumann, the Pereskioideae and the Cereoideae under the Cactaceae, which is as it should be. However, in the 9th/10th edition of the same work (1924) these two subfamilies are replaced by two new subfamilies of Vaupel, the Malacospermae and the Sclerospermae, formally incorrect in endings, worthless from the systematic point of view, and untenable as to priority. Vaupel's clean-cut affirmation that priority has no place in the classification of the Cactaceae (in Engl. & Prantl, Nat. Pflanzenf., ed. 2, **21**: 613. 1925) must be seen to be believed in. In these, and countless other abuses of every nomenclatural principle, is clearly read the notion, known only to some outside of Germany, but there to all appearances widely current, that the names above the genus do not apply to anything in particular, and may be handled at will.[15] It is not surprising that most modern authors upon dealing with these names choose to be discreet, to use them anonymously, or under the cover of some authority, who frequently happens to be as reliable as those I have cited. The facts justify the statement that today we are fairly agreed on the use of the units between the species and the genus, but as yet very much at sea in the use of those below the species (especially if typical) and above the genus.

Under the current Rules, the rank of a subtribe, tribe, subfamily and family is automatically determined by the ending, whether *-inae*, *-eae*, *-oideae*, or *-aceae*. This standardization has obvious advantages, but is not free from unwelcome results in practice. What is to be done with a name, legitimate in its ending for a certain rank, which has been erroneously placed as to rank by its author at publication? For example: Mueller Argoviensis

[15] This strange belief, for all I know, might hark back to a distinction which, apparently current before 1737, can be traced to the pages of Linnaeus' *Critica Botanica*. In this work, the names of Classes and Orders (modern Orders and Families) are said to be *muta* (silent), while those of Genera, Species, and Varieties are described as *sonora* (loud) (op. cit. 6; Phil. Bot. 158. 1751). That this distinction is academic can readily be seen, where Linnaeus states (op. cit. 138; Phil. Bot. 199. 1751) that the names of Classes and Orders have identically the same status as those of Genera. Beliefs rooted in custom die very hard; it may be suspected that a great deal of the current lack of feeling for trinomials, and many "philosophical" discussions about the use of subspecies and variety stem from thought once accepted in the American Code of 1904, and since dead in appearance rather than in fact.

published the Pereae as a subtribe. Subtribes must end in -inae, hence Mueller's name is now untenable in the subtribal rank. This name, on the other hand, is tenable for a tribe, for it ends in a legitimate manner in *-eae. Shall we honor the ending of the name in preference to its originally designated rank, or the other way around?* Shall we accept the Pereae of Mueller as good for a tribe because the name ends in *-eae,* or shall we reject it, because Mueller definitely intended it to stand at publication for a subtribe? As a third possibility, shall we undertake to correct the Pereae of Mueller, having this name read Perinae, still crediting the authorship to him with reference to the original publication?

The Rules do not provide a direct answer to these questions. Although I have ventured my opinion on them in the footnote of a previous paper (Ann. Mo. Bot. Gard. **29**: 355. 1942), I feel that a full discussion of the matter is still in order, and that some data may properly be contributed here on the score.

Whether corrections are acceptable, to have names like Mueller's Pereae turned into Perinae, with reference to the original publication and Mueller's authorship unchanged, seems to me to be a matter still subject to personal preferences. As such, this matter can be settled only by a free vote in Congress. The principle it involves—I should like to point out—is important, nevertheless, and not to be tampered with lightly.

The current Rules frown upon corrections which are not absolutely required by previous patent errors or misprints (Art. 59, 70, 71), and if modifications of the kind now under discussion are to be allowed, suitable modifications will have to be introduced in the Articles in question. Authors careful of the integrity of original citation, moreover, may not be inclined to alter names, crediting them to authors who never coined them as a straight matter of record. My feeling is that if anything must stand corrected, it is better to correct the rank, leaving the name itself unchanged, for it is to the name sooner than to the rank that the author's name is immediately attached. Corrections restricted to the rank, at any rate, will not lay hands upon the generalities now in the Rules about what may be corrected, and how. This, in my opinion, is a paramount consideration.

Considering that one of the fundamental Articles (Art. 4) requires that useless names be not published, and that names and forms be rejected which may cause confusion and error, I believe that by far the best possible solution is to accept, for instance, Mueller's Pereae as a tribe, disregarding Mueller's own designation of it as a subtribe. By so doing, we avoid publishing once again the Pereae and placing the original Muellerian entity of the same name in the synonymy of the subtribe Perinae. The simplification in reference and citation attending this procedure is patent. It may be feared by some that the honoring of names *on their endings,* that is, accepting

Mueller's Pereae as a tribe, may lead to numerous nomenclatural changes. The danger, in my opinion, is not great: we merely shall accept the Pereae Muell. Arg. (1866) in place of the Pereae Pax & Hoffm. (1931). Authorships, consequently, are apt to be involved sooner than anything else. Few will be the cases in which the name itself will undergo a change, as when, for instance, the Tithymaloideae Vent. (1799), takes the place of the Crotonoideae Pax (1890). Naturally, when using a name published by an earlier author with a change of rank it will be necessary to acknowledge the fact for the sake of a full and correct citation. This can easily be done by following Tithymaloideae Vent., used as a subfamiliar name, with a standard abbreviation, such as p.o. (*pro ordine*). Changes in the names of families are now almost impossible, for, as it is well known, we are bound by a list of *nomina familiarum conservanda* (Syn. Propos. Nomencl. Sixth Intern. Bot. Congr. 64. 1935; Proc. Sixth Intern. Bot. Congr. **1**: 358. 1936). The omissions in this list (Aizoaceae or Mesembryanthemaceae, for instance) may readily be remedied.[16]

Names originally proposed in the forms of a language which is neither Latin nor Greek are another source of confusion. Article 7 in the Rules which is supposed to speak in the matter, and is often referred to in discussion, is ambiguous. It reads: "Scientific names of all groups are usually taken from Latin or Greek. When taken from any language other than Latin, or formed in an arbitrary manner, they are treated as if they were Latin. Latin terminations should be used so far as possible for new names." This Article gives no examples, but refers, if I am not mistaken, to such names as *Macaranga* and *Ouratea*, *Schinus Molle* and *Quercus Tozza*, which, although neither Latin nor Greek in origin are to be treated as if they were of the classic languages. It cannot be construed to legitimize and protect such names as Péridées of Baillon, even less Luxembourgiés of Van Tieghem, because, unlike Baillon, Van Tieghem made it a point not to use Latin endings, setting his own standards up in defiance of those of every other botanist. It is patent, moreover, that Péridées does not end in *-eae*, and this automatically makes it illegitimate under Art. 24.

Granted that Art. 7 requires elucidation and proper restating, it may well be that the best way out of the difficulties created by the presence of names in the taxonomic record with French, German, and other such endings, which conflict with Art. 23 and 24, consists in a legitimization of current usage. Current usage undoubtedly tends to honor these names, so long

[16] Sprague's discussion (Jour. Bot. **60**: 69. 1922) is probably the reason why the most important of these names have been omitted from this list. I firmly believe that Sprague's contentions are ill digested and disturbing to sound nomenclature. The influence which they have exerted will not long be hidden from a thoughtful reader of the notes of Melchior (E. & P. Nat. Pfl. **21**: 109, footnote. 1925) and Krause (op. cit. **15**(a) 224, footnote 2. 1930). Although Melchior agrees with Sprague, and Krause dissents, all these authors act with a full disregard of the existing rules of nomenclature.

as they have been published with a description and have priority. The Actinidiacées of Van Tieghem, for instance, (Jour. de Bot. **13**: 173. 1899) have been indorsed as Actinidiaceae by Gilg & Werdermann (in Engl. & Prantl, Nat. Pflanzenf. ed. 2 **21**: 36. 1925) and Rehder (Man. Cult. Trees Shr. ed. 2. 630. 1940).

Failure to accept these names as if published in the proper Latin form may ease the solution of some nomenclatural problems, but is certainly bound to complicate the definition of others, possibly more important. The list of the *nomina familiarum conservanda* in vigor insures taxonomy against unwelcome changes in the major units of classification, and a simplification in nomenclature is always most desirable. Accordingly, an addition should be made to Art. 23 and 24 to state that names above the genus are to be honored (if otherwise validly and legitimately published) which bear endings in French, German, or other modern languages, readily assimilable to the correct Latin forms *-inae*, *-eae*, *-oideae*, and *-aceae*. The wording of such an addition is difficult. Formal proposals will be made in the future, if possible, in order to cover the changes suggested as needed in this study.

SUMMARY

This study consists of two parts, as follows:

(A) An historical review of the fundamental literature between the years 1735 and 1789, in which artificial and natural classification were at last clearly understood, and ultimately separated. Additional data are offered for the period between 1789 and 1905. The following works and dates are suggested as crucial, (1) Linnaeus' *Systema Naturae*, 1735; *Methodus Sexualis*, 1737; *Classes Plantarum*, 1738; (2) Adanson's *Familles des Plantes*, 1763; (3) Lamarck's *Flore Françoise*, 1778; (4) Antoine Laurent de Jussieu's *Genera Plantarum*, 1789. The revitalizing influence upon systematic thought of Bernard de Jussieu, who, although publishing nothing in botany, laid out in 1759 the plants of the garden of the Trianon according to the natural method of classification is underscored. Comments are specifically offered upon the works of Gleditsch, 1764; Haller, 1768; Necker, 1790; Ventenat, 1799; Jaume-St. Hilaire, 1805; A. P. De Candolle, 1805.

(B) A consideration of issues of practical nomenclature in the units above the genus. Doubts and confusions now prevailing in the handling of these units are pointed out. It is suggested that names published between the genus and the class be honored on their endings, disregarding, if necessary, the original designation of rank, and that names of the same nature published with formally improper endings in languages other than Latin be legitimized.

THE ARNOLD ARBORETUM, HARVARD UNIVERSITY
JAMAICA PLAIN, MASSACHUSETTS

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 72, NO. 1, PP. 76–85 JANUARY, 1945

EFFECT OF COTTON ON THE GERMINATION OF PHYCOMYCES SPORES[1]

WILLIAM J. ROBBINS AND MARY BARTLEY SCHMITT

In earlier studies in this laboratory (2, 3, 4, 5) on the germination of spores of *Phycomyces blakesleeanus* a drop of a spore suspension was placed on an agar medium in a Petri dish measuring 15 × 100 mm. Each dish contained 10 ml. of the agar medium. After from 3 to 18 hours incubation, depending on the rapidity of germination, spore counts were made under the low power of a compound microscope. This method of studying the effect of various substances on spore germination has certain advantages. The spores are held in position on the agar medium; complete sterility, if desirable, is easy to maintain; the spores are exposed to the air; the dishes are convenient to handle. It has certain disadvantages also. The agar used should be especially purified (6) and it could perhaps interfere by adsorption or otherwise with the activity of some types of substances which are under investigation. If many substances and concentrations are studied the space occupied by the dishes becomes a factor to be considered. Furthermore, the 10 ml. of medium used in a dish requires more material than is desirable if the substance to be tested is available in limited amounts. Smaller Petri dishes measuring 15 × 60 mm. and containing 2.5 ml. of medium solidified on one side of the dish were substituted for the larger ones with satisfactory results.

Use of 1 ml. of Medium in Spot Plates. More recently use has been made of Pyrex plates, 85 × 100 mm. in size, with 9 concave depressions, 22 mm. in diameter and 7 mm. deep (fig. 1). These depressions conveniently hold 1 ml. of medium and it is possible to run nine different media on a single plate. This method has all the advantages of an agar medium in a Petri dish and is economical of space and material. The procedure in our experiments was as follows:

The basal agar medium consisting per liter of 1.5 g. KH_2PO_4, 0.5 g. $MgSO_4 \cdot 7\ H_2O$, 50 g. dextrose, 1.0 g. asparagine, 500 mμ moles thiamine, and 10 g. purified agar[2] was sterilized in 10-ml. quantities in a 20 × 150-mm. test tube, tube (A) in figure 2. The supplements whose effect on germination was to be studied were sterilized in about 0.2 ml. of distilled water in a test tube,

[1] This research was supported in part by Mr. Manfred Wahl, whose kindly and intelligent interest the authors are pleased to acknowledge.

[2] To this the following mineral supplements in p.p.m. were added: 0.005 B, 0.02 Cu, 0.10 Fe, 0.01 Ga, 0.01 Mn, 0.01 Mo, and 0.09 Zn.

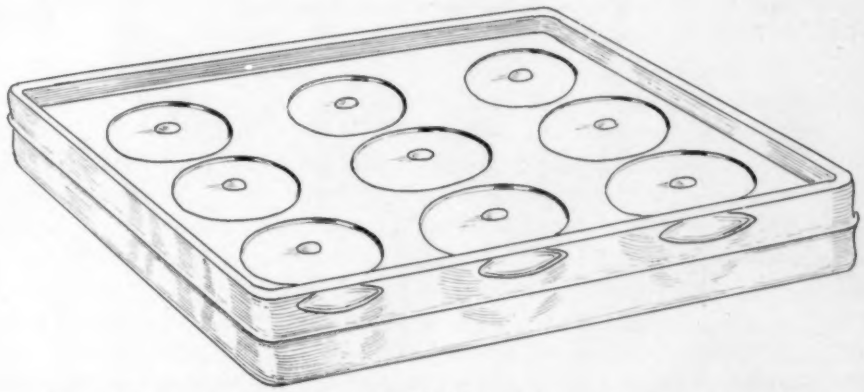


FIG. 1. Pyrex spot plate. Each depression contains 1 ml. of an agar medium, and one drop of spore suspension has been placed on each spot.

tube (B) in figure 2. After sterilization 1 ml. of the melted basal agar medium from (A) was added with a sterile pipette to the 0.2 ml. of liquid containing the supplement in (B). After mixing, the agar was poured into a depression in the plate which had been previously sterilized. If no supplement was used the basal medium was mixed with 0.2 ml. of distilled water separately sterilized in (B). When the agar had solidified in the depression a drop of spore suspension in sterile distilled water was placed on the surface of the agar by means of a platinum loop about 3 mm. in diameter. The inoculated plates (fig. 1) were piled one on another, the top one covered with a piece of glass or an empty plate, and placed in a moist chamber for incubation at from 25° to 26° C. Eight hours were selected as a convenient and satisfactory time for incubation. At the end of that time the plates were set in a refrigerator and held until the next day for counting.

Results with Hypoxanthine and a D_r Fraction. When this method[3] was used, *Phycomyces* spores from cultures from 6 to 9 days old showed 1 per cent germination or less on the basal medium. The addition of hypoxanthine or of a D_r fraction prepared from potato[4] increased the germination slightly. However, hypoxanthine and the D_r fraction together had a marked effect (table 1). In the presence of 5.0 mg. of the D_r fraction the activity of 0.1 mμ mole (0.0136 μg.) of hypoxanthine could be observed. The effect of the hypoxanthine increased up to 50 mμ moles per ml. and decreased with larger amounts.

Although the results within a single experiment were consistent the per cent germination for a particular combination of hypoxanthine and the D_r fraction was not duplicated in successive experiments. For example, when

[3] Absorbent cotton was used for plugging the tubes in these experiments. See later discussion.

[4] The preparation of this fraction is described by Robbins and Hamner (4).

TABLE 1. *Effect of hypoxanthine and a D_r fraction from potato on germination of Phycomyces spores*

	No addition	0.5 mμ mole hypoxanthine	5.0 mμ moles hypoxanthine	5.0 mg. D_r	0.1 mμ mole H + D_r	0.5 mμ mole H + D_r	1.0 mμ mole H + D_r	5.0 mμ mole H + D_r	10.0 mμ mole H + D_r	50.0 mμ mole H + D_r	100.0 mμ mole H + D_r	1000.0 mμ mole H + D_r
Exp. 1	1	.....	4	5	9	15	28	.....	58	63	53	22
Exp. 2	1	.....	4	8	.....	23	31	.....	80	83	78	.....
Exp. 3	1	2	3	8	14	28	47	68	.....	.....	.....	.....
Exp. 4	<1	1	3	3	20	41	54	87	.....	.....	.....	.....

1.0 mμ mole of hypoxanthine and 5.0 mg. of the D_r fraction per ml. were used the per cent germination varied in four successive experiments from 28 to 54. We are unable to account for this variation. The per cent germina-

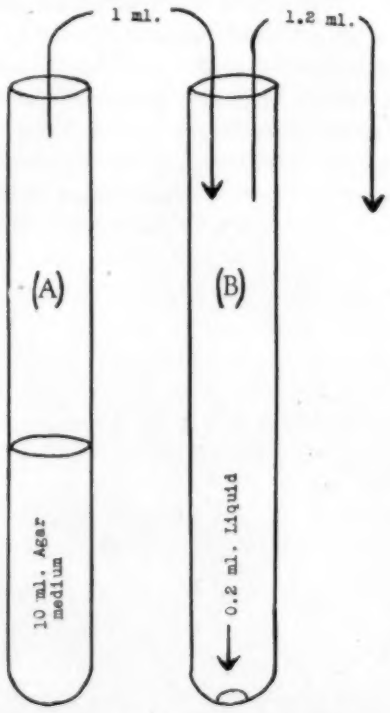


FIG. 2. For explanation see text.

tion is affected by the age of spores, temperature of incubation, and time of incubation as well as by the composition of the medium, but we were not able to select any variable which could account for the differences between experiments to which attention has been called.

Effect of Cotton Plugs. However, an inconsistency in one of our experiments led to the discovery that under certain conditions the cotton used in plugging the test tubes materially influenced the results. Since this observation may be of more general interest than for the study of the germination of *Phycomyces* spores it seemed worth while to report our results.

The experiment which led to this discovery was as follows:

Certain supplements whose effect was to be studied were used with the basal agar medium containing 5 mμ moles of hypoxanthine per ml. In some instances the supplements were autoclaved in 0.1 or 0.2 ml. of distilled water in test tubes (B) plugged with ordinary cotton. One ml. of the agar medium from tube (A) containing 10 ml. was added to the small amount of liquid containing the supplements in tube (B) and the mixture poured into a depression in the plate. The germination ranged from 16 to 44 per cent. In other instances the supplements were sterilized in 10 or 15 ml. of distilled water and 0.1 or 0.2 ml. of this liquid were mixed with 1 ml. of the agar medium in an empty dry sterile tube before it was poured into the depression in the plate. The germination ranged from 2 to 5 per cent. It appeared therefore that beneficial material was extracted from the walls of the test tube or from the cotton plug of tube (B). When all the active material obtained from a test tube was added to 1 ml. of medium the beneficial effect on germination was marked. When one-fiftieth or less of the extract from a test tube was included with 1 ml. of medium, as occurred when the supplements were sterilized in 10 or 15 ml. of distilled water, the effect was negligible.

Effect of Glass of Test Tube. We first suspected that something might have been dissolved from the glass of the test tubes during autoclaving. Since the test tubes were cleaned with chromic acid–sulfuric acid cleaning mixture, we thought traces of chromic acid left in the tubes were removed by autoclaving and concentrated in the small amount of liquid in the bottom of tube (B). New test tubes were rinsed with distilled water, 0.1 ml. or 0.2 ml. of distilled water were added to each tube, the tubes were plugged with ordinary cotton and autoclaved. The same procedure was followed with old tubes which had been cleaned with chromic acid cleaning mixture. After autoclaving some of the old tubes were rinsed with distilled water, 0.1 ml. or 0.2 ml. of distilled water were placed in each tube, the old plugs were replaced and the tubes resterilized. One ml. of agar medium from a 10 ml. quantity was added to each tube. In one set of experiments the basal medium was used and in another the basal medium plus 5.0 mμ moles of hypoxanthine per ml.

Both old and new test tubes yielded extracts which were beneficial with the agar medium containing hypoxanthine (table 2). The tubes autoclaved twice with rinsings between autoclavings yielded extracts distinctly beneficial though less so than those autoclaved once. The extracts were ineffective

TABLE 2. *Per cent spore germination when media given were mixed with distilled water autoclaved in test tubes stoppered with cotton*

	Basal medium tube (A)		Basal medium plus 5.0 mμ moles hypoxanthine per ml. in tube (A)	
	0.1 ml. distilled water in tube (B)	0.2 ml. distilled water in tube (B)	0.1 ml. distilled water in tube (B)	0.2 ml. distilled water in tube (B)
New test tubes	4	3	30	30
Old test tubes	4	2	33	38
Old tubes autoclaved twice with rinsing between	3	2	20	18

in the basal medium without hypoxanthine and it appeared immaterial whether the quantity of liquid autoclaved in tube (B) was 0.1 or 0.2 ml.

Effect of Various Kinds of Cotton. Since little difference was observed between the effect of old or new tubes an experiment was performed in which the tubes (A) containing the agar medium (basal medium plus 5.0 mμ moles hypoxanthine per ml.) were sterilized without plugs, with plugs of ordinary cotton, or with plugs of absorbent cotton. The tubes (B) containing 0.2 ml. of distilled water also were autoclaved open, plugged with ordinary cotton or plugged with absorbent cotton. No difference was noted between the open tubes containing 10 ml. of the agar medium and those plugged with cotton. Whenever tubes (B), containing the 0.2 ml. of distilled water, were plugged with ordinary cotton the per cent germination was high (table 3). It appeared, therefore, that material beneficial to spore germination was extracted in autoclaving a test tube plugged with ordinary cotton batting. One-tenth of the material extracted from a single plug was ineffective. This conclusion followed because 1 ml. of the 10 ml. of basal medium from tubes A plugged with ordinary cotton was inactive. The material was not extracted from plugs of absorbent cotton.

TABLE 3. *Effect of autoclaving open tubes or plugged tubes on per cent germination of Phycomyces spores*

Tubes (A) of basal medium autoclaved	Tubes (B) with 0.2 ml. distilled water autoclaved	Per cent germination
Open	Open	5
Open	Plugged ordinary cotton	55
Open	Plugged absorbent cotton	5
Plugged ordinary cotton	Open	4
Plugged ordinary cotton	Plugged ordinary cotton	54
Plugged ordinary cotton	Plugged absorbent cotton	6
Plugged absorbent cotton	Open	5
Plugged absorbent cotton	Plugged ordinary cotton	42+
Plugged absorbent cotton	Plugged absorbent cotton	7

Further experiments showed that the beneficial material was extracted under the conditions given above from freshly ginned cotton, from "sanitary" cotton, but not from "aseptic non-absorbent" cotton.[5] We found also that it was not always necessary to use a small amount of liquid in the test tube (B) during autoclaving. Sufficient water of condensation was sometimes formed during autoclaving an empty tube plugged with cotton so that the beneficial effect could be observed after the basal medium had been added to such a tube.

Location of the Beneficial Material in the Test Tube. Since the 1 ml. of agar medium was added to a test tube (B) containing 0.2 ml. of liquid and then poured into a depression in the Pyrex plate it appeared possible that the beneficial material might have come either from the small amount of liquid in the bottom of a tube (B) or from the lip of the tube which was in contact with the cotton during autoclaving. Our experiments showed that the beneficial material was in the liquid and did not come from the lip of the tube. This was demonstrated by autoclaving 0.2 ml. of distilled water in open tubes or in tubes plugged with ordinary cotton. The basal agar medium plus 5.0 mμ moles of hypoxanthine per ml. was added to both types of tubes. The agar from one set of tubes (B) plugged before autoclaving was poured into the depressions in a Pyrex plate so that it ran over the lips of the tubes. The agar from another set was removed with a pipette and had no contact with the lips of the tube. The per cent germination for the agar prepared with the open tube was 2; for the agar poured out over the lip was 34; and for that removed with a pipette, 33.

Source of the Beneficial Material. It was noted that the small amount of liquid in a stoppered tube usually contained a few strands of cotton which fell from the cotton plug. It was found, however, that these strands were not responsible for the beneficial material which was apparently distilled by steam from the plug into the tube during autoclaving. This was demonstrated by comparing the activity after autoclaving of tubes (B) plugged in the customary way with cotton, open tubes in which a few strands of cotton were placed in the 0.2 ml. of distilled water in the bottom of the tube, and tubes stoppered with plugs wrapped with cheese cloth which had been thoroughly washed. The liquid from the open tubes in which a few strands of cotton had been placed was not active, and that from tubes plugged with the wrapped plugs was nearly as effective as that from the tubes plugged in the ordinary way.

[5] The sanitary cotton is described by the manufacturer as thoroughly washed, free of black specks and lint; a good grade of cotton for routine bacteriological work.

The aseptic non-absorbent cotton is described as absolutely sterile, a high-grade material used for plugging bacteriological apparatus.

The assumption that the active material was steam-distilled from the cotton plug was confirmed by the following experiment. About 3.0 g. of air-dry cotton were placed in a condenser. Dry steam passed up through the cotton was condensed and collected. During the distillation steam was run through the jacket of the condenser containing the cotton so that the current of steam passing through the cotton did not condense. Used with the basal medium plus 5 mμ moles hypoxanthine per ml., a 0.2-ml. portion of the first part of the distillate consisting of 8 ml. gave 20 per cent germination, as compared to 5 per cent without the extract, 0.2 ml. of the second portion (3.5 ml.) of the distillate gave 9 per cent, and 0.2 ml. of a third portion (1 ml.) 7 per cent. The per cent germination obtained with the liquid in a plugged tube containing 0.2 ml. of distilled water was 27. It appeared from this experiment that the active material was volatile with steam and that most of it was extracted from 3 g. of cotton in the first 8 ml. of distillate. The 8 ml. in the first distillate was obtained from 3 g. of cotton and 0.2 ml. was tested. Therefore, the extract of about 0.07 g. of cotton obtained in this way favorably affected the germination of *Phycomyces* spores. The distillate was water-clear and had a pH of 3.9.

Additional Observations on the Active Material. Further experiments which will not be detailed here demonstrated the following: No active material was observed in the distillate when 100 g. of moist cotton were placed in a flask with 100 ml. of distilled water and the water was partially distilled by heating the flask in a bath of saturated NaCl. Moist cotton dried at 100° C was still active. The active material was not destroyed or driven off by heating dry cotton at 50° or 100° C for 7 days. An active solution was obtained by autoclaving at 14 lbs. for 1 hour an 8-quart stainless-steel kettle containing 58 ml. of distilled water and plugged with 580 g. of cotton. The extract was water-clear and had a pH of 5.0. In the basal medium, on which 2 per cent germination was observed, 0.1 ml. of this extract (equivalent to 1.0 g. of cotton) gave 25 per cent and 0.2 ml., 46 per cent germination. The active material was not lost when a solution was evaporated to 1/100 its original volume. It disappeared when dried over night (about 18 hrs.) at 50° C or for 2½ hours at 100° C. Most of the activity disappeared with 45 minutes drying at 100° C. When an active extract was neutralized with NaOH and dried at 50° or 100° C over night, most of the activity remained.

Attempts to determine dry matter of the unneutralized extract were unsuccessful. For the neutralized extract from tubes plugged with cotton we found the extract from 1 g. cotton contained 0.034 mg. of dry matter. The extract obtained with the stainless steel kettle contained 0.017 mg. of dry matter per g. of cotton.

Active Material Compared to Hypoxanthine and D_r Fraction. The material extracted from the cotton plugs appeared to contain little or no

hypoxanthine or a substitute therefor. It acted in part like the Z_2 factor (contained in the D_r fraction from potato tubers). This is indicated by its inactivity[6] in the basal medium lacking hypoxanthine (tables 2, 4) and relative ineffectiveness in the basal medium supplemented with the D_r fraction only (table 4). The extract from a single plug in a test tube containing 0.2 ml. of distilled water was more effective on germination than 0.5 mg. of the D_r fraction and less effective than 5 mg. of the D_r fraction. This conclusion follows by comparing the germination obtained with a plugged tube (B) on a medium containing 5 mμ moles of hypoxanthine (51%) with that obtained with open tubes (B) on a medium containing 5 mμ moles of hypoxanthine and 0.5 mg. of the D_r fraction (31%) and that containing 5 mμ moles of hypoxanthine and 5 mg. of the D_r fraction (65%).

Table 4. *The effect of cotton plugs in tube (B) compared with no plugs on germination of Phycomyces spores on basal medium plus supplements as given*

	None	1 mμ mole hypoxanthine	5 mμ moles hypoxanthine	0.5 mg. D_r fraction	5 mg. D_r fraction	1 mμ mole hypoxanthine plus 0.5 mg. D_r fraction	5 mμ mole hypoxanthine plus 0.5 mg. D_r fraction	1 mμ mole hypoxanthine plus 5 mg. D_r fraction	5 mμ moles hypoxanthine plus 5 mg. D_r fraction
No plug	1	2	5	2	12	11	31	65	79
Plug	2	17	51	4	20	39	74	70	89

The active material obtained with dry steam from cotton differs from the D_r fraction in having little effect on the growth of the germ tubes. Its action was limited to increasing the germination. It cannot, therefore, be considered to be equivalent to the D_r fraction except in its effect on spore germination.

Active Material Considered as an Organic Acid. The properties of the active material suggest that it is an organic acid perhaps adsorbed by the cotton and freed from it by dry steam. The active extracts from cotton were slightly acid; the active material could be concentrated by evaporation but was volatile on drying at 50° or 100° C unless neutralized. These characteristics would agree with those of an organic acid.

Furthermore, organic acids beneficially affect the germination of *Phycomyces* spores as has been previously reported from this laboratory (5) and the effective quantity of propionic acid (and perhaps acetic acid) was found to be of the same order of magnitude as the dry matter determined in active extracts of cotton studied in this paper. Although it required 1 mg. of sodium

[6] The extract increased the per cent germination in the absence of hypoxanthine if used in amounts equivalent to 10 g. or more of cotton.

acetate in the basal medium to produce the same effect as the extract from a cotton plug (about 1.0 g. of cotton) in the presence of hypoxanthine the quantity of acetate necessary was between 0.025 and 0.050 mg. Sodium propionate was more effective than sodium acetate (table 5). One mg. of the propionate in the basal medium was more effective than the extract from a cotton plug and in the presence of hypoxanthine the quantity of propionate required was between 0.005 mg. and 0.010 mg. We found 0.034 mg. of dry matter per plug in the extract obtained from plugged tubes and 0.017 mg. per g. of cotton in the extract obtained with the steel kettle. These figures are in the same class with the amounts of propionate and acetate active in affecting the germination of spores of *Phycomyces*.

TABLE 5. *Per cent germination of Phycomyces spores in the presence of various amounts sodium acetate or sodium propionate in the basal medium and the basal medium plus 5 mμ moles of hypoxanthine per ml.*

Mg. of sodium salt per ml. medium	Na acetate	Na acetate and 5 mμ moles hypoxanthine	Na propionate	Na propionate and 5 mμ moles hypoxanthine
1.000	25	92	55	98
0.050	< 1	36	2	85
0.025	< 1	12	2	75
0.010	< 1	7	1	44
0.005	< 1	2	1	16
0.000	< 1	1	< 1	1
Plugged tube	.....	28	.....	28

It should be added that both the cotton extracts and the organic acids had little influence on growth and the activity of each was greater in the presence of hypoxanthine than in its absence.

DISCUSSION

We have previously reported (6) that thiamine, biotin, and pyridoxine are present in cotton and may be extracted in amounts sufficient to affect the growth of microorganisms if, during autoclaving, water of condensation drips through the plugs into the medium. This rarely occurs and may readily be observed by noting whether the plugs are wet or dry after autoclaving. In the experiments reported here the active material was extracted by the steam in the autoclave; no liquid passed through the cotton plugs, which were entirely dry after autoclaving. This source of growth-promoting material is of no significance in many experiments but it may be a serious source of error in others.

In our experiments plugs made of absorbent cotton or of aseptic non-absorbent cotton did not yield sufficient material to influence the response we were studying and one-tenth of the quantity obtained during autoclaving

from a plug of ordinary cotton was below the limit of activity detectable by our methods.

In studies of the sporogenes growth factor Knight and Fildes, in a paper quoted by Knight (1), found it necessary to wrap the cotton wool plugs in washed gauze to prevent cotton fibers dropping into the culture medium, which would have given sufficient contamination of active substance from the fibers to vitiate the experiment. Wrapping the plugs in our experiments did not prevent active material entering our culture media as we prepared it. Sherwood and Singer (7) found folic acid to be present in cotton and they suspected cotton plugs to be a source of error in their experiments.

Our observations and those of others emphasize the necessity of considering in any experiments with microorganisms the role that cotton may play and of making certain by appropriate means that substances derived from the cotton used in stoppering the apparatus are not a complicating factor.

SUMMARY

A method of studying the germination of spores of *Phycomyces blakesleeanus* using 1 ml. of agar medium in spot plates of Pyrex glass is described. Extracts favorably affecting spore germination were obtained by autoclaving cotton-plugged tubes. The active material was distilled from the cotton plugs by dry steam. It was not removed by heating moist or dry cotton at 100° C. It was thermostable and could be concentrated in water solution by evaporation. It disappeared on drying an active solution at 50° or 100° C unless the solution was neutralized. It is believed to be an organic acid adsorbed by the cotton and freed by dry steam.

NEW YORK BOTANICAL GARDEN
AND
DEPARTMENT OF BOTANY, COLUMBIA UNIVERSITY
NEW YORK

Literature Cited

1. **Knight, B. C. J. G.** Bacterial nutrition. Material for a comparative physiology of bacteria. Special report. Series No. 210; 182 pg. Privy Council Medical Research Council, His Majesty's Stationery Office, London, 1936.
2. **Robbins, William J.** Effect of extracts of *Phycomyces* upon its development. Am. Jour. Bot. **27**: 559–564. 1940.
3. ————. Further observations on factor Z. Bot. Gaz. **102**: 520–535. 1941.
4. **Robbins, William J. & Hamner, Karl C.** Effect of potato extracts on growth of *Phycomyces*. Bot. Gaz. **101**: 912–927. 1940.
5. **Robbins, William J., Kavanagh, Virgene Wasbritton & Kavanagh, Frederick.** Growth substances and dormancy of spores of *Phycomyces*. Bot. Gaz. **104**: 224–242. 1942.
6. **Robbins, William J. & Ma, Roberta.** Vitamin deficiencies of *Ceratostomella*. Bull. Torrey Club **69**: 184–203. 1942.
7. **Sherwood, Marion B. & Singer, Eileen D.** Folic acid in cotton. Jour. Biol. Chem. **155**: 361–362. 1944.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 72, No. 1, pp. 86–113 JANUARY, 1945

A MORPHOLOGICAL AND CYTOLOGICAL STUDY OF A NEW FORM OF VOLVOX—I*

JEROME METZNER

INTRODUCTION

Although *Volvox* has been investigated frequently since its discovery by Leeuwenhoek (1700), many gaps in our knowledge of it remain. The need for extended comparative studies, especially of living material, has been emphasized by Pascher (1927), who maintains that a thorough and exact observation of the *Volvox* forms of different countries must be preliminary to monographic treatment of the genus. In addition, Pascher concludes that even the European species of *Volvox* have been described unsatisfactorily.

Few investigations have been made on American species of *Volvox* since the pioneer work of Powers (1907, 1908). Pocock (1933a, b), however, has illustrated the morphology and life history of South African species with unusually clear photographs and descriptions of living material. The only detailed account of mitosis and meiosis in *Volvox* is that of Zimmerman (1921) on *Volvox aureus*. Because division figures even in abundant material are difficult to find, this aspect of research on *Volvox* has been neglected.

The organism—*Volvox Carteri*—considered in this paper has been reported by five other workers, Powers (1908), Shaw (1922c), Iyengar (1933), Playfair (1918), and Apte (1936), from widely separated parts of the world since its original description by Carter (1859) from Bombay, India. These reports are limited to the more obvious details of morphology.

METHODS

The morphological aspects of this paper are based primarily on detailed observations of living material. The abundance of *Volvox Carteri* permitted observations over long periods. Temperature and pH determinations were made at the source from time to time, and various other ecological factors were noted. The organisms were concentrated by means of a small plankton net. Water draining from the net was collected in large glass jars into which *Volvox* colonies were later introduced. Some of the concentrated *Volvox*

* The second part of this study, containing the cytological and taxonomic portions, will appear in a subsequent issue of the Bulletin. All the figures for both parts appear with part I. The list of literature cited in both parts will appear with part II.

A grant from the Lucien M. Underwood Memorial Fund provided assistance in the publication of the figures.

material was fixed at the time of collection, and some subsequently at hourly intervals in Flemming's weak solution, Iodine-formalin solution (Johansen 1940), Chrom-acetic solution, Allen's B15 solution, and Navaschin's fluid. For cytological study, Flemming's solution gave the best results. All processes up to sectioning were carried on in shell vials which were ultimately broken to release the imbedded material. Sections were cut 5 μ, 7 μ, 10 μ and 12 μ thick, and these were stained in the following solutions: Heidenhain's iron-alum haematoxylin, Flemming's triple stain, Newton's gentian violet, Safranin, and the Feulgen stain. Of these, a short method employing Heidenhain's iron-alum haematoxylin gave the best results in general. Newton's gentian violet was excellent for revealing the structure of the pyrenoids, but it was ineffective as a nuclear stain. The Feulgen nucleal reaction was especially helpful in tracing changes occurring within the nucleus during the mitotic cycle, and served to confirm the mitotic picture observed after staining with Heidenhain's iron-alum haematoxylin. Fast green was used as a counter-stain.

Oospores in various stages of development were picked up with a fine pipette and placed in a small slot cut into a jelled agar plate. Fixative was added (usually Flemming's weak) and the slot was sealed by pouring molten agar over it. After this had jelled, a small agar cube containing the fixed oospores was cut out of the plate and placed into a vial containing fixative. Subsequently, the agar blocks were treated as were the *Volvox* colonies described above. Because oospores contain much stored food material, they blacken considerably after Flemming fixation. Prolonged bleaching in H_2O_2 or chlorine water was therefore employed.

Membrane studies were made on living colonies treated with dilute methylene blue, according to the method of Meyer (1896), and also on stained, microtomed sections.

ECOLOGICAL DATA

Volvox was found abundantly in large tanks[1] approximately 15 feet long, 5 feet wide, and 1 foot deep containing pond lilies, and less frequently in those in which *Sagittaria*, *Lotus*, or *Pistia stratiotes* was growing. As might be expected, the amount of *Volvox* available at any given time varied considerably from tank to tank. In some, growth was so rich that the water looked green, whereas others nearby contained relatively few colonies. Varying conditions within the tanks were responsible for differences in growth rates and cycles. Changing of the seed plants in the tanks, changes of water, disinfections and removal of algae such as *Hydrodictyon* probably affected the growth of *Volvox*.

[1] I am grateful to William Tricker Inc. for generous consideration in permitting me to have free access to tanks located at Saddle River, Bergen County, New Jersey.

Volvox occurred in water ranging in temperature from 27° to 33° C, but most often at about 28°. These water temperature readings were taken at the surface. Readings taken at the bottom of the tanks were 5° to 9° C lower.

In bright sunlight the *Volvox* colonies exhibited a strong thigmotactic response to leaves and stems of the plants associated with it. Pond lilies or other plants were, at times, covered with dense green accumulations of colonies on the surfaces of the submerged parts. If the pond lilies were disturbed, the *Volvox* became free swimming but returned later to cover the leaves and stems.

The pH of water containing *Volvox Carteri* was fairly constant, ranging usually from 7.2 to 7.5.

CULTIVATION

Zimmerman (1921) kept *Volvox aureus* for three months and *Volvox globator* for ten months in 1–6-liter glass containers of source water covered up to the water line with black paper to prevent lateral illumination. Pocock (1933b) did not succeed in establishing vigorous permanent *Volvox* collections, and depended upon the abundant natural material available. Uspenski and Uspenskaja (1925) found that *V. minor* (*V. aureus*) and *V. globator* have a relatively high iron requirement, and devised a culture medium in which the organism could be maintained for prolonged periods. Other workers (Knoke 1924, Mainx 1929a, b, Pringsheim 1930, Lefèvre 1932) have reported techniques for the culture of *Volvox*. These contributions indicate that continuous cultivation of *Volvox* in the laboratory is difficult.

Culture experiments were attempted with the following types of solutions:

1. Uspenski's fluid (Uspenski and Uspenskaja 1925).
2. Bold's soil extract #2 (Bold 1936).
3. Source water.
4. Source water plus iron salts (0.5 mg. Fe_2O_3 per liter).
5. Source water plus Uspenski solution (20%).
6. Source water plus Fe salts (0.5 mg. Fe_2O_3 per liter) plus KNO_3 (0.5 gm. per liter).
7. Uspenski solution with citrate buffer (potassium citrate added in concentration of 0.004 M per liter).
8. Moewus' solution (10%) (Moewus 1940).

At first, for each of these solutions three series were set up: (1) single asexual colonies in 25 ml. of solution, (2) 15–25 asexual colonies in 25 ml. of solution, (3) large numbers of all types of colonies in 100 ml. of each solution. From the initial experiments it was found that only solutions 1, 3, 5, and 8 were somewhat successful, and in these only the third series containing large initial numbers of *Volvox* managed to maintain themselves for any appreciable time. Best results were obtained from the use of Uspenski's solution full strength or a combination of source water and

Uspenski's solution (20%). During the latter part of July, August, and early September *Volvox* was maintained in these solutions in quart jars placed on the broad sill of an east window. Here cultures received direct sunlight only during the morning hours and indirect light the rest of the day. It was necessary to add some additional Uspenski's fluid (25–50 ml.) or a few drops of its component $FeSO_4$ solution every week. When collections were left in their original source water, they soon degenerated. Apparently, therefore, species of *Volvox* differ in their ability to grow under laboratory conditions. Some, *V. aureus* and *V. globator*, persist for some time in source water (Zimmerman 1921); others, *V. Carteri*, *V. Rousseletii*, and *V. capensis*, perish within a few days (Pocock 1933b); the life of some species, *V. Carteri*, *V. minor*, and *V. globator*, is prolonged in culture by regular addition of iron salt (Uspenski & Uspenskaja 1925); light and temperature are also important factors. In spite of numerous experiments, it was not possible to maintain *V. Carteri* indefinitely in culture in the laboratory.

MORPHOLOGY AND LIFE HISTORY

The membrane structure of *V. Carteri* resembles to a remarkable degree that of *V. tertius* Meyer described by Pocock (1938) and is similar to that of *V. gigas* Pocock and *V. africanus* Rich & Pocock in general plan of structure.

A common colony membrane encloses the peripherally placed cells (figs. 37, 39). Directly outside the apex of each protoplast the common membrane is slightly depressed, and through the floor of this depression the two flagella project. Dilute methylene blue used on living material (fig. 97), as well as on paraffin sections, reveals the structure of the membrane and of the interior of the coenobium (fig. 92). Each protoplast occupies the outer portion of a pentagonal, hexagonal (most commonly), or heptagonal gelatinous prism with a dome-shaped outer membrane lying just below the common colony membrane (figs. 39, 41, 55). The prisms taper slightly toward their inner limits, which are bounded by slightly curved membranes. Gelatinous[2] material occupies the space between the dome-shaped membranes of the prisms and the periphery of the colony. Within each coenobium there is present a somewhat alveolated, amorphous gelatinous material denser near the prisms and much less dense or absent at the center. Each protoplast of reproductive cells is surrounded by a closely adhering cell membrane and is enclosed within a wide saccular vesicle formed by the enlarged prism membrane extending into the interior of the mother colony (figs. 51, 52). Pocock (1933a) states that in *V. gigas* "the cells of the young embryo are not enclosed in a common membrane" and

[2] The word gelatinous is used to indicate the physical rather than the chemical nature of this material.

mentions earlier in the same paper that the common envelope is formed after inversion. Her illustrations do not show a common colony membrane in pre-inversion daughters of *V. africanus*, but in her paper on *V. tertius* (1938) figure 2c shows what is apparently a common colony membrane in a daughter about to invert, although this structure is not mentioned in the textual discussion of this stage. In *V. Carteri* the common colony membrane (presumably derived from the cell membrane of the original gonidial protoplast) is clearly evident (fig. 92) even in the early stages of gonidial division. It is closely attached to the underlying cells, whereas the prism membrane, forming a wide vesicle around the developing daughter, extends into the interior of the mother coenobium, and is there limited by the internal gelatin or by vesicular membranes of developing sister colonies. After the gonidia sink beneath the surface of the parent colony, their gelatinous prisms swell to such an extent that their original polygonal shape is lost, and as the daughters develop within them, they enlarge and occupy almost all of the hollow central cavity of the parent colony.

Powers (1908), Iyengar (1933), and Apte (1936) noted that there is a gradual diminution from the anterior to the posterior pole of the colony in the distances between neighboring protoplasts in the forms of *V. Carteri* they observed. This is also evident in the organisms of the present study. The protoplasts at the anterior poles of the adult colonies are more widely separated than those at the posterior pole (figs. 94–96).

Because the coenobia are not exactly spherical, but somewhat ovoid, nor the protoplasts evenly spaced, estimations of cell members in colonies can be only coarse approximations. Janet's (1923a) method of squaring the number of cells counted on a great circle and then multiplying by 0.318 was used in estimating the number of cells in coenobia. There is some difficulty in counting accurately the cells in a great circle. Other methods have been used by Klein (1889a), Zimmerman (1921), and Shaw (1922b), but Janet's method seems to be simple and fairly accurate. A summary to be presented later includes data on cell numbers.

Volvox colonies contain, in general, two types of cells: (1) purely vegetative cells, (2) reproductive cells. The latter participate in reproductive processes in addition to carrying on all vegetative processes, with the exception of contributing to motility of the parent. The reproductive cells are sometimes interpreted as specialized cells, whereas they are really more primitive physiologically than the vegetative cells. They have retained their capacity to perform all fundamental life functions (with the exception of motility), including that of reproduction, whereas the purely vegetative cells have become specialized by losing their capacity to reproduce. In *Volvox* colonies, therefore, the majority of the cells are physiologically specialized and relatively few; the reproductive cells remain physiologically

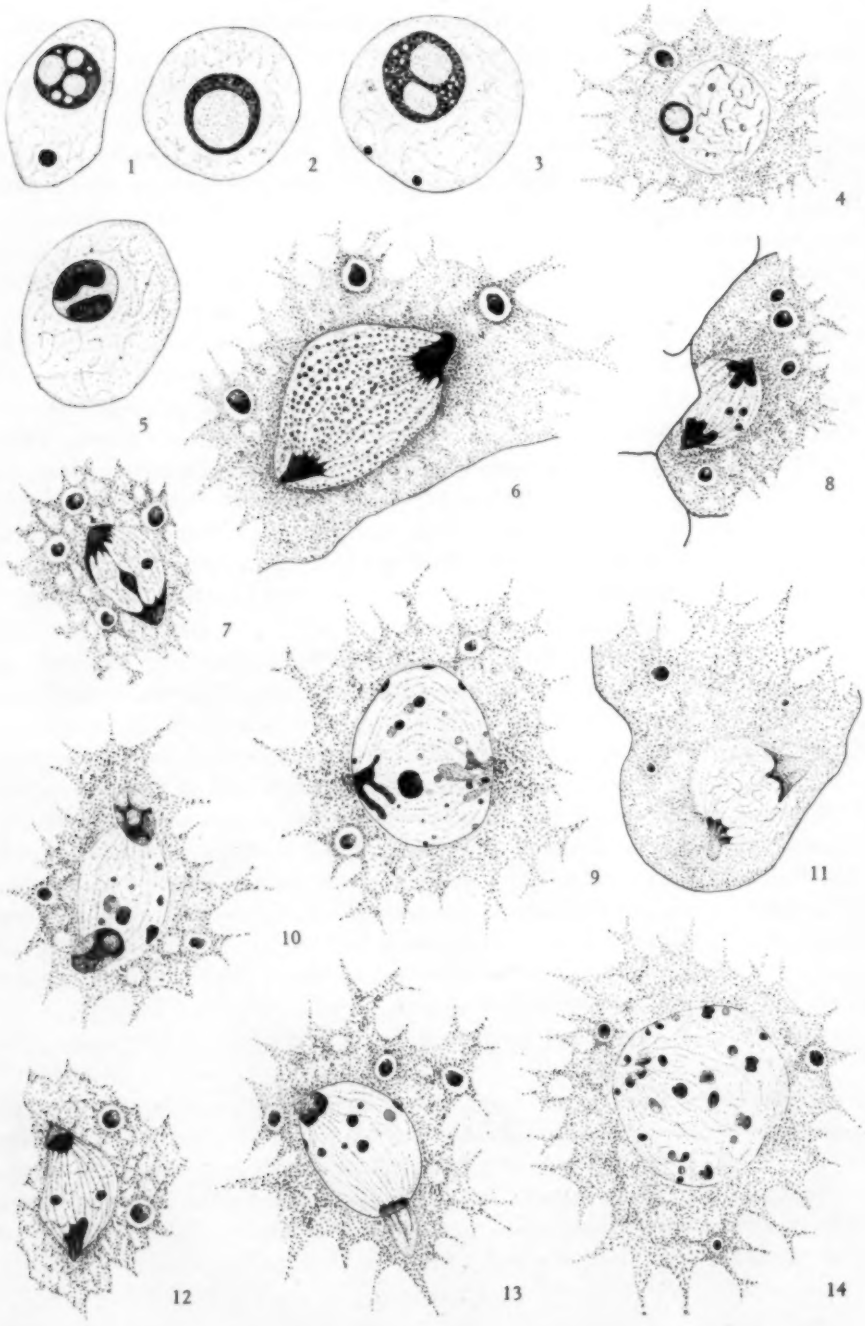
primitive, but they have undergone morphological differentiation which adapts them to their special reproductive functions.

Protoplasts of purely vegetative cells are distinctly *Chlamydomonas*-like, and in adult colonies are not connected by protoplasmic strands. Each is contained within a gelatinous wall in the form of a polygonal prism bounded by membranes (figs. 37, 42, 56). A large cup- or bowl-shaped chloroplast occupies the base and sides of the protoplast, but does not extend completely to the apex, thus leaving a clear area. At the base of the chloroplast is a large pyrenoid (infrequently two) consisting of a spherical center surrounded by from two to six (usually four) starch plates (fig. 40). Figure 117 shows division of a pyrenoid. This would seem to indicate that pyrenoids arise from preexisting pyrenoids by division, but does not preclude the possibility that some arise *de novo* as various workers have reported (Overton 1889; Zimmerman 1921). Within the upper hollow portion of the chloroplast lies the nucleus (3–4 μ) with its endosome prominent even in the living condition. Two separated flagella, from two and one-half to three times the length of the protoplast, arising from refringent granular blepharoplasts at the apex of the protoplast, project through the prism and common colony membrane to the exterior. Two contractile vacuoles, alternately expelling their contents, are also located in the colorless apex. The investigations of Mast (1907, 1919, 1922, 1926, 1928, 1932) have added much to our knowledge of the structure and function of the eyespot (stigma) in *Volvox* and related organisms. Pocock (1938) states that the stigma, in all species of *Volvox* as yet investigated, lies in the posterior prolongation of the chloroplast and is usually situated symmetrically in relation to the points of insertion of the two flagella. In the anterior polar region of the material here studied the stigma lies about a third of the length of the cell from its apex. As the distance from the anterior pole increases, the position of the stigma rises, while its size decreases, until at the equator of the colony the eyespot is reduced to a minute speck at the apex of the cell. In the posterior part of the colony there are no eyespots (figs. 94–96). One or more highly refractive bodies, vibrating back and forth in Brownian movement, frequently occur near the stigma (fig. 37). Pocock (1938) also found these in *V. tertius* and identified them as volutin.

In coenobia crushed by cover glass pressure certain vegetative cells at the torn portions of the colony frequently become free-swimming. Their resemblance to *Chlamydomonas* is remarkable. No attempt has been made, as yet, to culture these cells nor to study their subsequent behavior. It is unlikely that such a phenomenon would occur in species with protoplasmic connections.

REPRODUCTION

Three types of reproductive cells occur, each in a separate colony: (1) Gonidia (daughter colony initials) which form daughter colonies by divi-


1
2
3
4
5
6
7
8
9
10
11
12
13
14

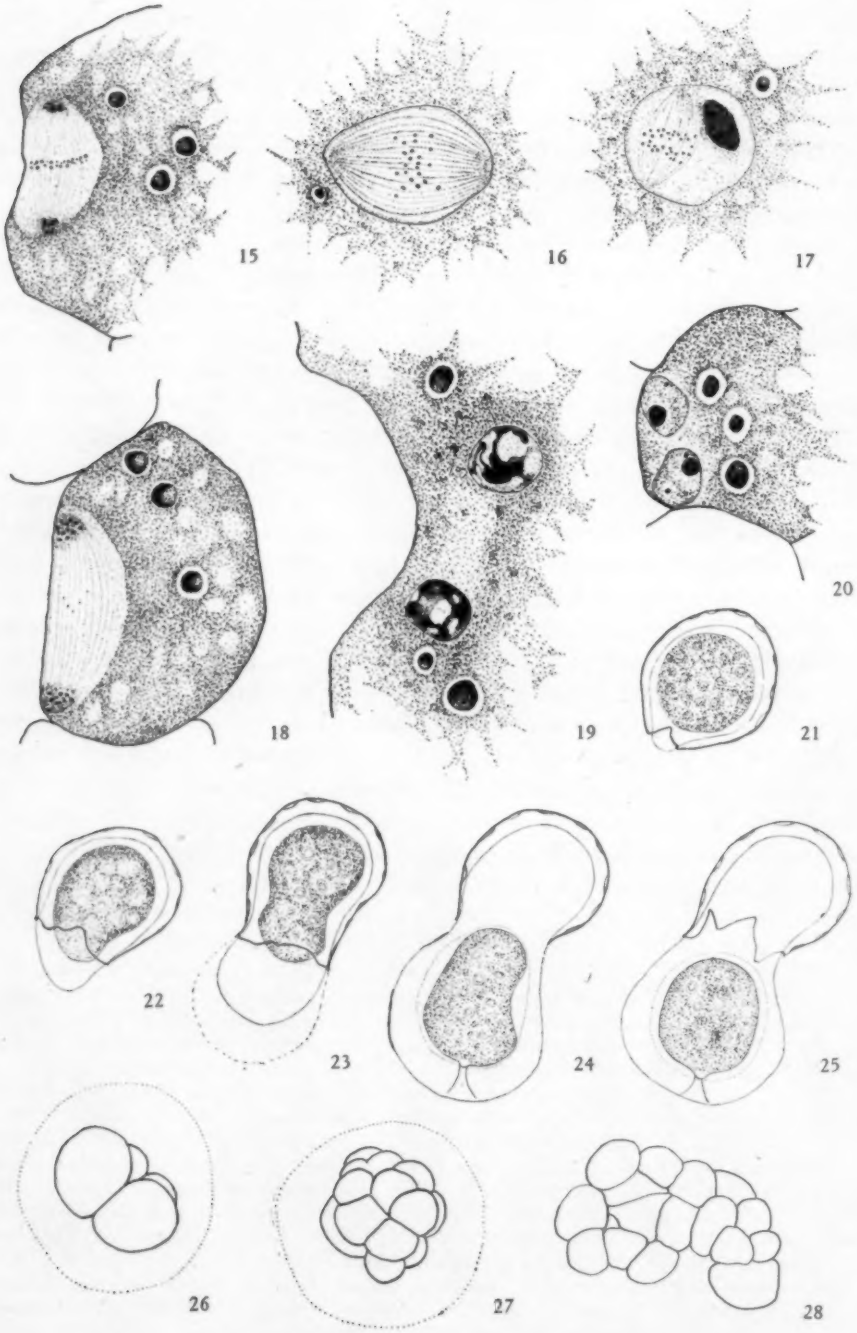
sion. (2) Female sex cells, each forming one oogonium and egg. (3) Male sex cells, each dividing to form a sperm platelet of 128 biflagellated sperms. All reproductive cells are biflagellated in their early stages of development. The flagella are lost as development and differentiation proceed.

Reproductive Cycle. Mother colonies may contain asexual, male, or female offspring, or combinations of these, except that the occurrence of males and females within the same mother has not been observed in *V. Carteri*. There seems to be a definite sequence in the types of daughters produced in a population. At the beginning of a cycle asexual daughters predominate for some time. Later males begin to appear and increase in number, while female colonies begin to occur still later. Asexual colonies are produced throughout the cycle, but the proportion of these varies, tending to diminish as the sexual stages flourish. At the height of the sexual phase of the cycle males and females occur in almost equal proportions. Shortly after, the proportion of males falls off rapidly while that of females remains high. Toward the end of the cycle the proportion of females may exceed that of asexual colonies (fig. 46), whereas practically no males can be found. The females then begin to disintegrate, settle down to the substratum and release their oospores as they break up. Only asexual colonies remain, and these initiate a new cycle. If environmental conditions are suitable, after a brief period of rest the oospores germinate. During the sexual phase, *Volvox* colonies are continually produced asexually. When environmental conditions become unsuitable, asexual production of colonies ceases almost abruptly, and the oospore undergoes a prolonged resting period until suitable environmental conditions are restored. Then germination of oospores occurs almost simultaneously, resulting in the production of large numbers of juvenile colonies (to be described later), and these give rise to the usual type of *Volvox* colony.

Explanation of figures 1–14

All of the drawings were made with the aid of a camera lucida using a Bausch and Lomb microscope with 10×, 43×, and 97× objectives in combination with various oculars. The photographs were taken with a Leica camera Model F. FIG. 4 ×970, others ×1200.

FIGS. 1–5. Nuclear division during interphase, endosomes in various stages of vacuolization. Note the nucleus with large vacuolated endosome and small plasmosome in figure 1. In figure 3 the nucleus contains two small chromatic bodies (plasmosomes?) in addition to the endosome. FIG. 6. Nucleus during prophase; polar masses are connected by granular threads. FIG. 7. Nucleus during prophase showing chromatic substance left behind after endosomal division. FIG. 8. Nucleus during prophase with lobed polar masses, chromatic granules persistent between them. FIG. 9. Nucleus during prophase showing early stages of extrusion of polar masses, the intranuclear portions with long fingerlike processes. FIG. 10. Nucleus during prophase with polar masses unlobed, ellipsoidal, vacuolated and partially extruded through the nuclear membrane. FIGS. 11–13. Nuclei during prophase with intranuclear portions of the polar masses deeply stained. FIG. 14. Nucleus during prophase with numerous chromatic bodies consisting of bivalent chromosomes, endosomal granules, and at the left an intranuclear portion of a polar mass.


15
16
17
18
19
20
21
22
23
24
25
26
27
28

Asexual Reproduction. Gonidia are differentiated at about the 64-celled stage of development of a daughter colony. All the reproductive cells ultimately reach a large size through growth. Once the gonidia are differentiated, they do not undergo subsequent division before the young colony is liberated from the parent. As they increase in size, the reproductive cells protrude into the interior of the colony until they occupy a position just below the peripheral row of vegetative cells, leaving behind a clear area, filled with gelatin, denoting their former position.

Gonidia are characteristically eight in number in a colony, occurring in two tetrad groups arranged in two parallel planes within the coenobium; one is just anterior to the equator and the other about half-way between the equator and the posterior pole (fig. 43). The members of one tetrad group alternate with the members of the other group. The precise mathematical arrangement of the tetrad groups has been stressed by Powers (1908) and Shaw (1922b). Gonidia remain biflagellated until after inversion of the developing colony. Inverting colonies, crushed under the cover glass, sometimes have a few of their gonidia torn free into the surrounding fluid and each possesses two flagella waving from a slightly depressed portion of the margin. The exact time of loss of these flagella could not be determined, but gonidia of everted and well developed daughter colonies no longer possess them. Usually, gonidia do not divide until after the extrusion of the daughter colony. Before division they attain about 80 μ in diameter. A mature gonidium is sharply characterized not only by its large size, but also by its highly vacuolated contents, prominent nucleus and numerous pyrenoids (figs. 49, 50). Vacuolization extends even to the chloroplast.

A detailed description of the stages of development of the gonidium of *V. aureus* prior to inversion has been given by Janet (1923b), and Pocock (1933b) has written a complete account of the inversion process in *V. Rous-*

Explanation of figures 15–28

FIGS. 15–19 ×1200. FIG. 15. Nucleus at early anaphase, traces of the polar masses persistent, chromosomes markedly condensed. FIG. 16. Nucleus during anaphase, polar masses no longer visible. (Not all the chromosomes are shown in this figure.) FIG. 17. Nucleus during anaphase, showing an undivided endosome lying outside of the spindle. FIGS. 18, 19. Telophases. FIG. 20. Interphasic daughter nuclei, endosomes and plasmosomes present. ×970. FIGS. 21–28. Germination of the oospore and development of the juvenile colony. ×430. FIG. 21. 9 Je 41. Oospore, mesospore protruding from ruptured exospore. 9: 30 a.m. FIG. 22. 9 Je 41. The same oospore at 10: 20 a.m. FIG. 23. 9 Je 41. The same oospore at 10: 35 a.m. FIG. 24. 9 Je 41. The same oospore at 11: 05 a.m.; the mesospore and protoplast have been almost completely extruded from the exospore. The delicate endospore is visible. Two flagella project from a colorless beak at the anterior end of the zoospore. FIG. 25, 9 Je 41. The same oospore at 11: 20 a.m. FIG. 26. 9 Je 41. 4: 30 p.m. The zoospore has lost its flagella and has undergone two divisions. FIG. 27. 9 Je 41. 7: 00 p.m. Further divisions have resulted in the formation of an irregular mass of cells. FIG. 28. Cell masses of developing juvenile colonies flattened by coverslip pressure.

seletii and *V. capensis*. Because division of the gonidium and development of the daughter colony of *V. Carteri* follow the general pattern described by these authors, only a brief description of the process will be presented in this study, with emphasis accorded to features peculiar to *V. Carteri*.

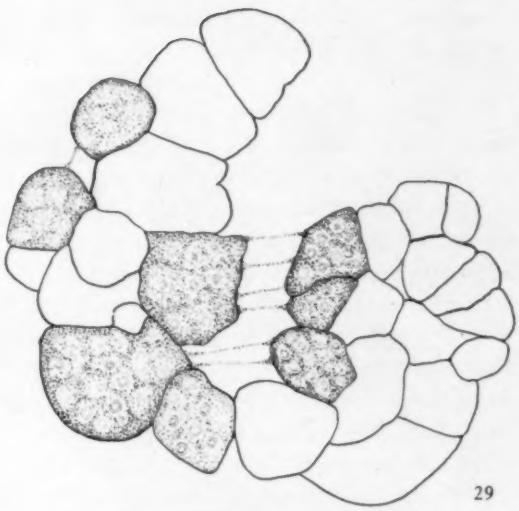
Gonidia begin to divide shortly after the release of daughter colonies from the parent coenobium. The plane of the first division is anticlinal (fig. 51). Both daughter cells are strongly incurved at the center of the plane of division, so that a hollow is formed between them (fig. 57). In the second division the plane is also anticlinal but frequently oblique to the first plane of division (figs. 52, 53).

The anterior physiological polar axes of the cells become progressively inclined toward one another as division proceeds (Zimmerman 1923) so that a characteristic bowl-shaped configuration is formed after the third division. This shape is maintained thereafter by anticlinal divisions. At the eight-celled stage of development (figs. 34, 35, 54) four of the cells slip below the remaining four. A shift in the physiological polar axes of these cells is brought about by reorientation of their contents, so that their axes become radii of the developing daughter. Figure 58 shows the 16-celled stage flattened by the cover glass. There are strong indications that the four large triangular peripheral cells divide later to form the eight gonidia of the next generation. This cannot be stated with certainty because it is difficult to trace individual cells beyond the 16-celled stage. Differentiation of the gonidial initials probably occurs at the 32- or 64-celled stage. In figure 36, approximately the 64-celled stage, the eight gonidia are clearly differentiated. Cells of the developing daughter colony divide synchronously with the exception of the differentiated reproductive cells. Cytological preparations show all the vegetative cells of a developing daughter colony in almost exactly the same stage of mitosis (fig. 100).

Cells of the developing colony have chloroplasts containing one or more pyrenoids. The colony is in contact with the external medium by means of the portion of the vesicle located on the surface of the mother colony. As division proceeds, the cells become progressively smaller and more compactly arranged. At this stage the phialopore is small and rests just below the

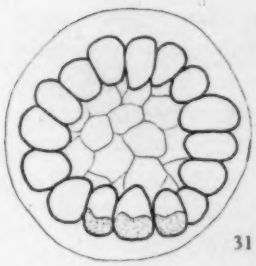
Explanation of figures 29–36

FIG. 29. Flattened juvenile colony showing protoplasmic connections between cells. ×860. FIG. 30. Bowl shaped juvenile colony formed fifteen to twenty minutes after the stage figured in 29. About four large reproductive cells bulge from the outside of the bowl which later everts. ×430. FIG. 31. Cup shaped developing sperm platelet before eversion. ×970. FIG. 32. Spermatozoid. ×970. FIG. 33. Curved sperm platelet. ×540. FIG. 34. 8-celled cruciate stage in the development of a daughter colony. FIGS. 34–36 ×970. FIG. 35. 8-celled stage in the development of a daughter colony. Four corner cells have slipped below the remaining four. FIG. 36. Approximately the 64 celled stage of development of a daughter colony. The eight reproductive cells of the next generation are already differentiated.



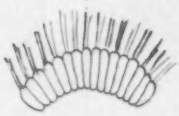
29

30

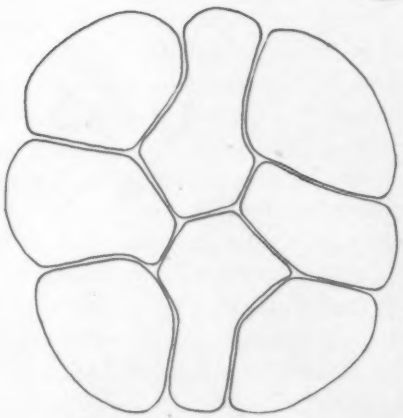


31

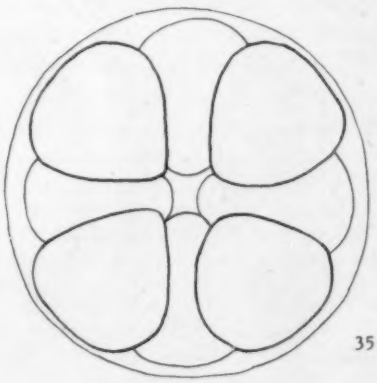
32



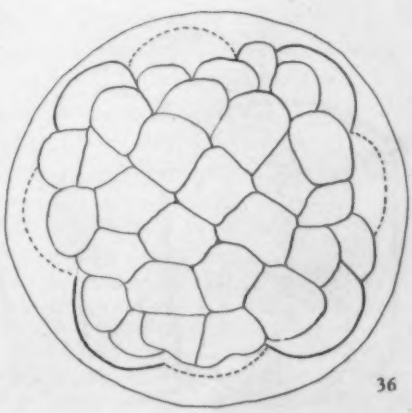
33



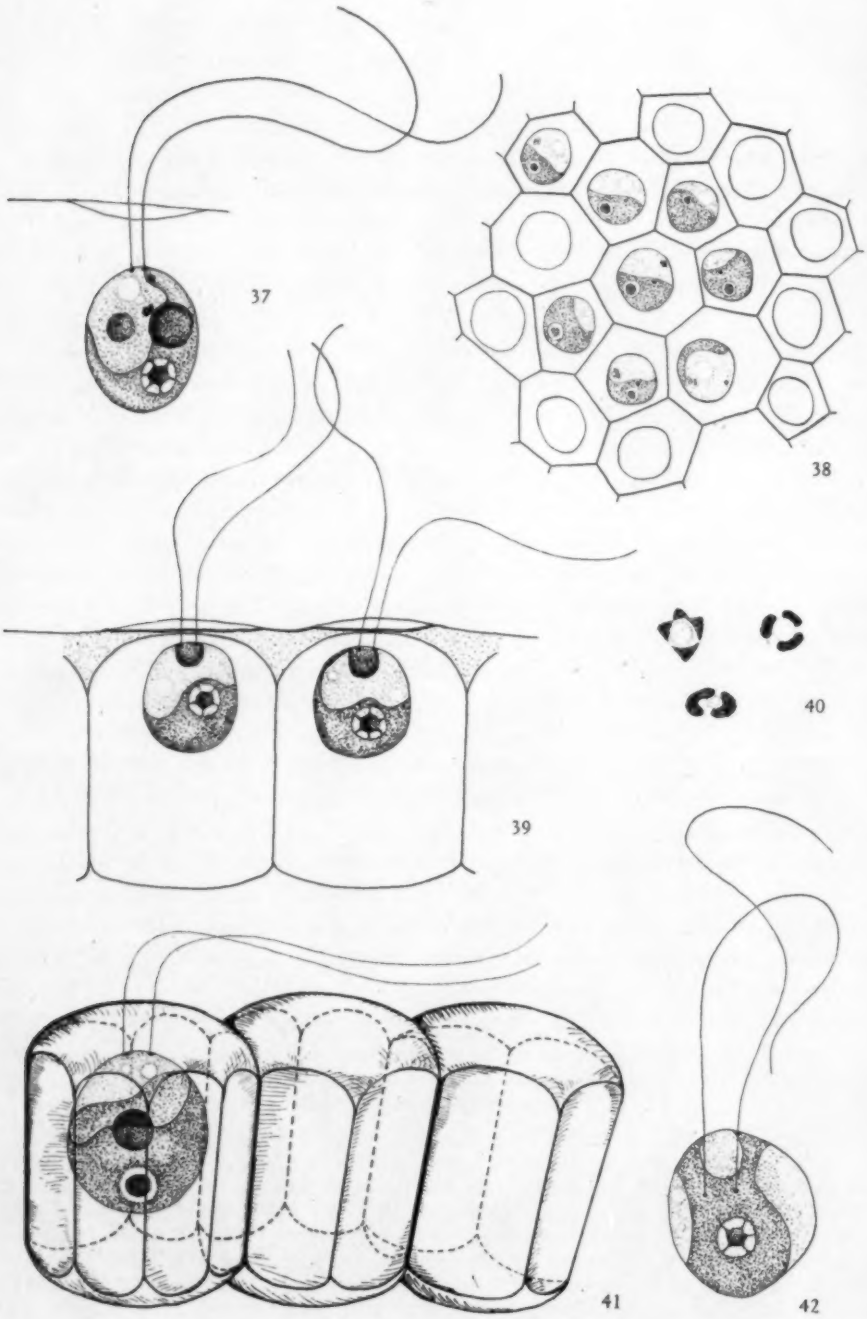
34



35



36


37
38
39
40
41
42

surface of the mother colony. Soon it becomes larger and irregular. In figure 63 the gonidia project outwardly from the surface and an enlarged phialopore is evident.

Inversion begins with a folding of the lobes (usually four) of the phialopore (fig. 59) into the hollow center of a daughter colony. At about the same time, the portion of the daughter directly opposite the phialopore begins to invaginate and continues to do so while the infolded lobes begin to straighten out. Pocock (1933) points out that changes in the shape of the cells, the appearance of flagella and protoplasmic connections at this time are essential factors in the inversion process in the forms she observed. The lobes of the phialopore become reflexed outward (fig. 60) over the exterior of the colony and proceed to fold over the colony until inversion is completed (figs. 61, 62, 64). Pocock (1938) was able to see protoplasmic connections in the cells of the phialopore lobes, and in some cells of the completely inverted daughters of *V. tertius* and *V. gigas*. In *V. Carteri* protoplasmic connections in recently everted daughters were seen on few occasions, but, as will be shown later, protoplasmic strands are clearly evident connecting the cells of developing juvenile colonies. After eversion, the lobes of the phialopore come together, fold over the pore and completely close it so that it can no longer be detected. An optical section (fig. 65) through the colony at this stage shows the well developed gonidia inside the colony. In surface view (fig. 66) the protoplasts are polygonal because of mutual compression and because the prism walls have not developed to any noticeable extent. At this stage stigmata appear, the flagella lengthen, the daughters increase in size and begin to move very slowly within their vesicles. Movement increases until rotation is distinct. Figure 47 shows two young colonies forced out of the mother by cover glass pressure and still enclosed by their vesicles. When fully mature, each colony escapes through the ruptured wall of the mother coenobium. Sometimes the mother colony breaks up after one or two daughter colonies have been discharged, thus releasing the remainder. Soon after birth, the gelatinous prism walls swell, separating the protoplasts which then lose their angular shape and become round in surface view.

Inversion occurs almost immediately after cell division is completed. Daughters in various stages of development and inversion were to be seen

Explanation of figures 37–42

FIG. 37. Protoplast of a vegetative cell. Note the common colony membrane. × 1455. FIG. 38. Group of 17 vegetative cells in surface view stained with methylene blue to reveal membrane structures. There are 4 pentagonal, 9 hexagonal and 4 heptagonal shaped cells visible. × 970. FIG. 39. Living vegetative cells in longitudinal optical section showing membrane structure. × 970. FIG. 40. Pyrenoids showing spherical centers with 2, 3 and 4 starch plates arranged around them. × 1200. FIG. 41. Schematic diagram of three adjacent *Volvox* prisms, 5, 6 and 7 sided to show the cell and membrane structure; colony envelope not shown. × 1900 approx. FIG. 42. Protoplast of an anterior vegetative cell. × 1940.

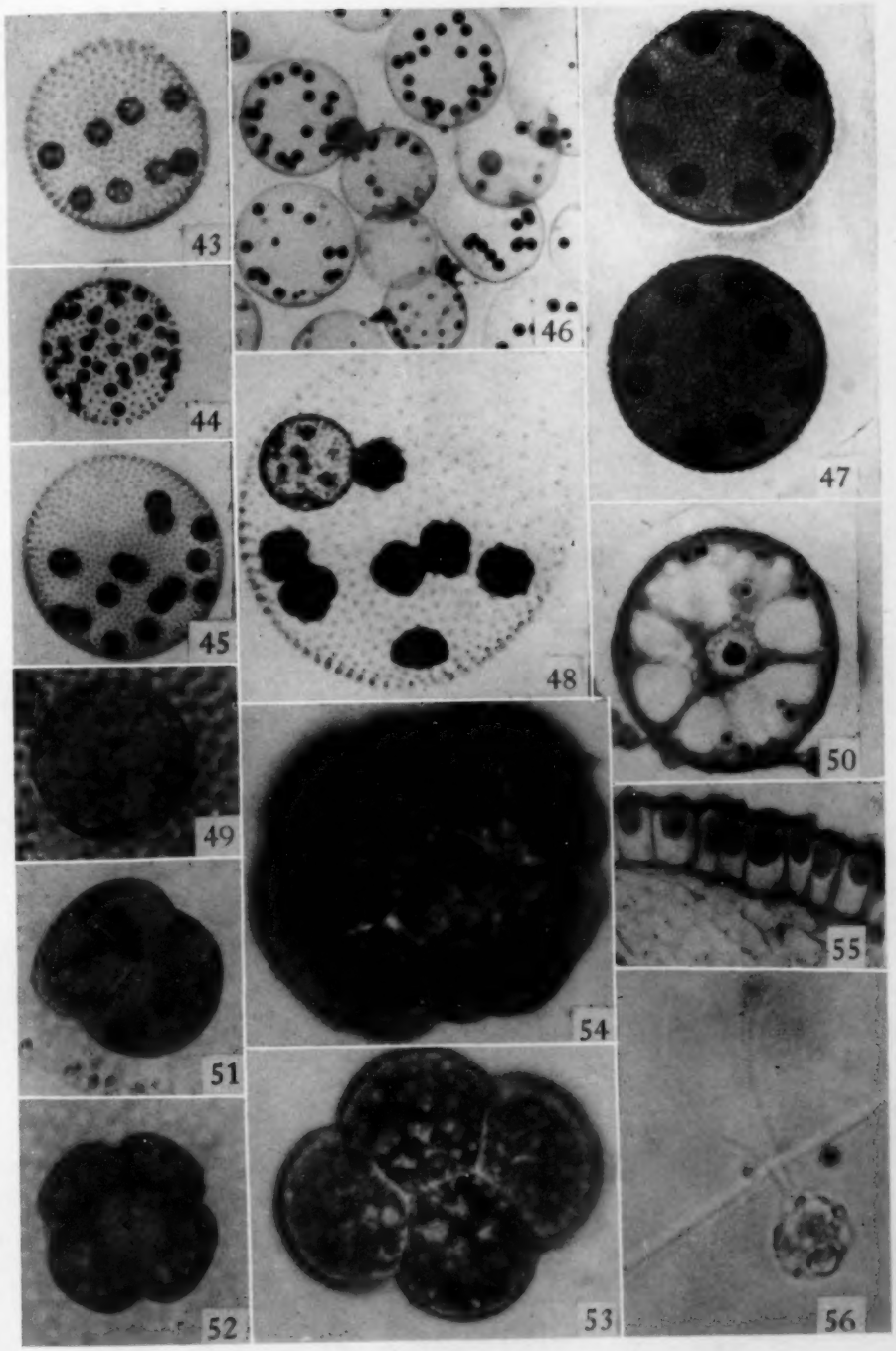
in samples of living *Volvox* taken at almost any time of the day or night. Later, in the cytological portion of this paper, it will be shown that there is evidence for two periods of maximum mitotic activity; one occurring in the afternoon at about 3 o'clock and the other in the evening at about 10 o'clock. Periods of maximum occurrence of inversion are directly correlated with these times of maximum cell division.

Sexual Reproduction. Just before birth, male colonies (fig. 44) are larger than either female or asexual colonies. After birth, however, there is little increase in size, whereas the other two types of colonies become considerably larger. The ultimate differences in size are due to the number of cells in each type of colony. Females have somewhat fewer cells than asexual colonies, but the males have from one-eighth to one-third the number of either of these.

Males are easily distinguished from the other two types of colonies by the relatively large number (50) of reproductive cells scattered all over each colony with the exception of a small area near the anterior pole (fig. 44). Asexual colonies have eight reproductive cells arranged in tetrads and female colonies have about 20 oogonia occupying the posterior two-thirds of the coenobium. Of all the types of reproductive cells, antheridial initials are the smallest and least differentiated from the vegetative cells. They lack the vacuolization of the gonidia and the dense protoplasm filled with storage material found in oogonia. Division generally begins just before the birth of the male colony and continues thereafter. Before division, a large number of pyrenoids have developed inside each antheridial initial. These become divided among the products of antheridial initial division until finally each spermatozoid possesses a single pyrenoid. Usually each

Explanation of figures 43–56

FIGS. 43–45 ×280. FIG. 43. Young asexual colony with 8 daughter colony initials. FIG. 44. Male colonies bearing numerous (about 50) sperm plate initials. FIG. 45. Mature female colony containing 16 oogonia. FIG. 46. Group of female colonies showing their predominance at the end of the sexual phase in the life cycle. ×130. FIG. 47. Young asexual colonies forced out of the mother colony by cover glass pressure, with their outer gelatinous membranes still intact. ×1000. FIG. 48. Asexual colony showing lack of synchronous development of daughter colonies. Of 8 developing daughters one is almost completely developed, while the others are in very early developmental stages. ×450. FIG. 49. Living daughter colony initial (gonidium). ×1000. FIG. 50. Sectioned and stained gonidium. Note the vacuolated protoplast in which several pyrenoids are scattered and the nucleus containing an endosome and plasmosome. ×2500. FIG. 51. First division of the gonidium; from living material. ×1000. FIG. 52. 4-celled stage of a developing daughter colony; from living material. ×1000. FIG. 53. 4-celled stage of a developing daughter colony; from living material. ×2400. FIG. 54. 8-celled stage of a developing daughter colony. ×2400. FIG. 55. Cytological preparation of a section through a group of vegetative cells of an adult colony. ×2500. FIG. 56. Vegetative cell, living condition. Note the pyrenoid at the posterior end, two contractile vacuoles at the anterior end, and flagella. ×5600.


43
46
47
44
48
45
50
49
55
54
51
53
52
56

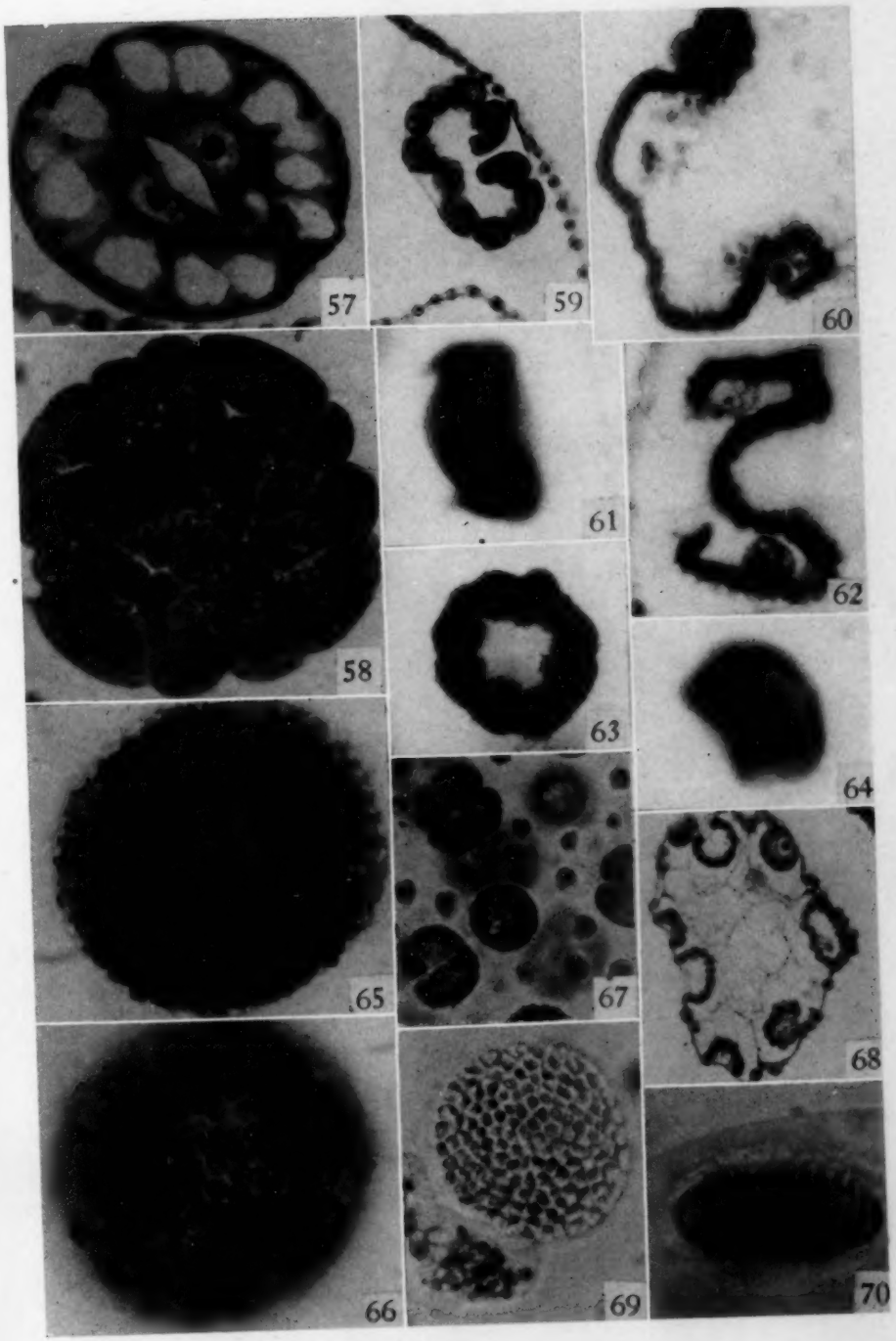
antheridial initial undergoes seven divisions resulting in a cup-shaped mass of cells (figs. 31, 67, 68, 69). Flagella appear during the inversion which immediately follows cessation of division. Sperm platelets are convex on their flagellated surfaces and concave posteriorly (figs. 33, 70). Shortly after inversion, the eyespots are formed. Spermatozoids appear like elongated vegetative cells (fig. 32). Each has a cup-shaped chloroplast, pale green in color, with a single pyrenoid located at the posterior end; two contractile vacuoles occur in the clear, pointed apical portion of the cell near the stigma and two flagella, approximately the same length as the body of the spermatozoid, project from the anterior tip.

When sperm platelets are mature, they begin to rotate within their vesicles as their flagella slowly beat. Flagellar movement increases until each platelet emerges through a pore in the external gelatin of the parent originally formed by the descending antheridial initial cell. All platelets are not released at the same time but over a period of time, during which the male colony is in vigorous motion. A short time after all the platelets have been released, the male colony usually breaks up. Once the platelet is free from the parent it moves rapidly through the water. The association of spermatozoids in a platelet is maintained for a prolonged period.

Female colonies (fig. 45) are only slightly smaller than asexual colonies and are distinguished from the latter by the larger number (usually 18 to 20) and specialized character of reproductive cells. As oogonia become differentiated in size from vegetative cells, they become greener, and their

Explanation of figures 57–70

FIG. 57. Cytological preparation of a section through the 2-celled developing daughter colony. Note the endosome and plasmosome in the nucleus of the cell on the left. ×2150. FIG. 58. 16-celled developing daughter colony flattened by cover glass pressure. Note 4 larger cells which will become reproductive cells. ×2400. FIG. 59. Median section through a developing daughter colony; beginning of eversion; phialopore lips and opposite pole invaginating. ×1000. FIG. 60. Median section through a daughter colony, color older than preceding. The phialopore lips now fold outward. Note the reproductive cell projecting from the outside of the colony (upper portion of figure). ×2100. FIG. 61. Lateral aspect of developing daughter colony; phialopore lips folding downward moving past the remainder of the colony (living material). ×1000. FIG. 62. Cytological longitudinal section of approximately the same stage of eversion as shown in figure 61. Note the large reproductive cells within the backfolding lips. ×2100. FIG. 63. Phialopore view of a living daughter colony before eversion. The large reproductive cells project from the outside surface. ×1000. FIG. 64. Lateral view, living daughter colony. Eversion process almost completed, the reproductive cells visible within the colony. ×1000. FIG. 65. Optical section through a living daughter colony after eversion. ×2900. FIG. 66. Surface view of a living daughter colony after eversion. The protoplasts are angular due to mutual compression. ×2900. FIGS. 67–70. Stages in the formation of a sperm platelet. FIG. 67. First and second divisions of sperm initial cells. ×1700. FIG. 68. Stained section through a male colony showing an initial cell and various stages in the development of sperm platelets. ×1000. FIG. 69. Immature sperm platelet after eversion in surface view, containing 128 cells. ×3800. FIG. 70. Lateral view of a mature sperm platelet; note eyespots and flagella. ×3800.


57
59
60
58
61
62
63
64
65
67
68
66
69
70

protoplasts become densely packed with storage material. In *V. tertius*, a species bearing strong resemblance to *V. Carteri*, the oogonia and gonidia have almost the identical vacuolated appearance. Oogonia of *V. Carteri* are sparsely vacuolated. In the living condition their dark green, opaque appearance is striking. Of the three types of reproductive cells produced by *Volvox*, the oogonium is the only one which does not undergo subsequent division. Janet (1922) found in *V. globator* a "blastéa oosphérienne" of 64 cells consisting of one large oosphere surrounded by an ephemeral syncytial follicle of 63 abortive oospheres which soon become resorbed without leaving a trace. There is no evidence that division of the female reproductive cell occurs in *V. Carteri*.

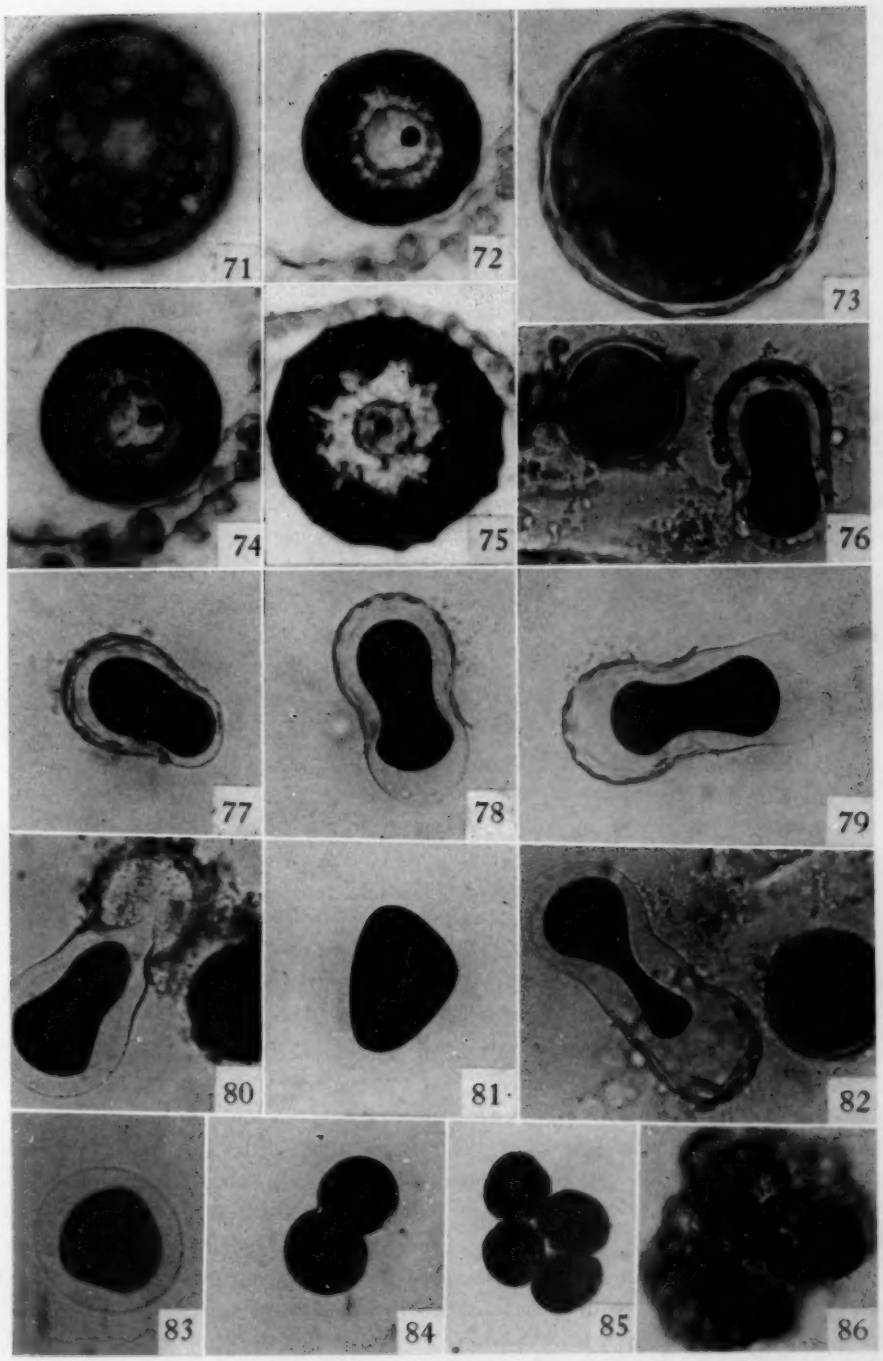
Mature eggs of *V. Carteri* (figs. 71, 72) are almost spherical, about 48 μ in diameter, and contain a great number of pyrenoids (larger than those of the vegetative cells), fatty globules, and material which responds positively to the chemical tests for volutin.

Although observations were made on many hundreds of female colonies containing oogonia in all stages of development, on no occasion were sperms found within the female colony or near the oogonia. In observations made on *V. perglobator* sperms were easily detected in close contact with the outer wall of almost any oogonium. Many of the sperms persisted on the outside long after the oospore wall had become differentiated. Microtome sections of *V. perglobator* show sperms on the periphery of oogonia and oospores. Overton (1889) and Lander (1929) have described male nuclei within the oosphere in *V. aureus* and *V. globator*, but Pocock (1933) believes that they may have been binucleate oospheres such as she observed in *V. Rousseletii*.

The fact remains that fertilization has not been authentically observed in any species of *Volvox*, although Zimmerman's (1921) description of zygotic meiosis in *V. aureus* indicates that it does occur. On the other hand, Mainx (1929a) showed that parthenogenetic development of eggs occurs commonly in *V. aureus*. Thus is would appear that eggs of *Volvox* may develop either parthenogenetically or after fertilization. It is possible that eggs may develop parthenogenetically in *V. Carteri*, but this cannot be stated with certainty.

Explanation of figures 71–86

FIG. 71. Optical section of a living oogonium containing storage material and pyrenoids. × 3000. FIGS. 72–75 × 2500. FIG. 72. Stained median section of an oogonium. FIG. 73. Living oospore in optical section. FIG. 74. Stained section through an oogonium showing a small nucleolus adjacent to the oogonium endosome. FIG. 75. Stained section through an oospore. FIGS. 76–82. Germination of the oospore. (Living material.) Note the cleft exospore, thick mesospore and delicate endospore in figure 80. × 1000. FIG. 83. Aplanospore surrounded by mesospore, endospore not visible, × 1000. FIGS. 84, 85. First and second divisions of aplanospore. × 1000. FIG. 86. Irregular mass of cells formed after further divisions. At the right one large reproductive cell is visible. × 2000.


71
72
73
74
75
76
77
78
79
80
81
82
83
84
85
86

Whatever their origin, the oospores become increasingly darker green and denser as they mature. Three walls or membranes are secreted by the developing oospore (figs. 73, 75): a delicate endospore closely attached to the protoplast, a rather thick mucilaginous mesospore, and finally, a tough exospore with a reticulately ridged surface. At first these membranes are indistinguishable, but after the oospore has matured, its protoplast contracts a little, showing the exospore and mesospore clearly. The endospore is usually so closely adherent to the protoplast as to be indistinguishable in the resting oospore, but it is frequently clearly evident during germination stages (figs. 24, 80). After the walls have been laid down, the oospore begins to change its color from dark green to an orange-brown. A fully ripened oospore has an exospore slightly wavy in outline because of surface reticulation, an underyling mucilaginous mesospore, and a centrally located orange-brown protoplast bounded by a close-fitting, delicate endospore. The orange-brown color of the oospore has been ascribed to the presence of an orange-red oil (Klein 1889a), carotin (Overton 1889; Zimmerman 1921), and to haematochrome (Pocock 1933b). When moribund females finally break up, their oospores are released and come to rest on the bottom. They germinate a short time later (see germination chart below) if conditions are favorable.

Cienkowski (1870) observed the production of aplanospores from germinating oospores of *V. aureus*. Zimmerman (1921) mentions that the external progress of germination of oospores of *V. aureus* is the same as described by Kirchner (1879), and reports that meiotic division occurs, resulting in the formation of a haploid aplanospore. Mainx (1929a) found that oospores were developed parthenogenetically in *V. aureus* under certain conditions, and that these parthenospores germinated in exactly the same fashion as described by Kirchner (1879) and Henneguy (1879). In oospore cultures of *V. Rousseletii* (Pocock 1933c) and of *V. tertius* (Pocock 1938) the first record of biflagellate *Chlamydomonas*-like zoospores was obtained by Pocock, who suggested (1938) the possibility that aplanospores are formed from parthenospores and zoospores from zygotes.

In attempting to obtain germination, moribund females were drawn up with a pipette from the bottom of a jar containing *Volvox* and placed into small petri dishes. Sometimes healthy females were removed from a mass collection and allowed to reach maturity in dishes containing one of the culture media employed in these experiments. In either case, after the female colonies disintegrated, the oospores were shed. Three types of fluid were used for germination experiments: (1) filtered water from the source in which *Volvox* was found; (2) Moewus' cold soil extract diluted as follows: one part extract, ten parts glass distilled water (Moewus 1940); (3) synthetic medium (Uspenski and Uspenskaja 1925). Spores from a given *Volvox* collection were separated into these three media at one time.

Germination occurred in solutions 2 and 3, but no germination occurred in solution 1 nor in certain combinations of the three solutions.

An effort was made to germinate dry spores, Pocock (1933b) having found with spores of *V. Rousseletii* and *V. capensis* that "completely drying was not essential but beneficial." In this study only wet spores were viable. A small percentage of germination occurred in Moewus' fluid, but about 90 per cent germination was obtained with Uspenski's fluid.

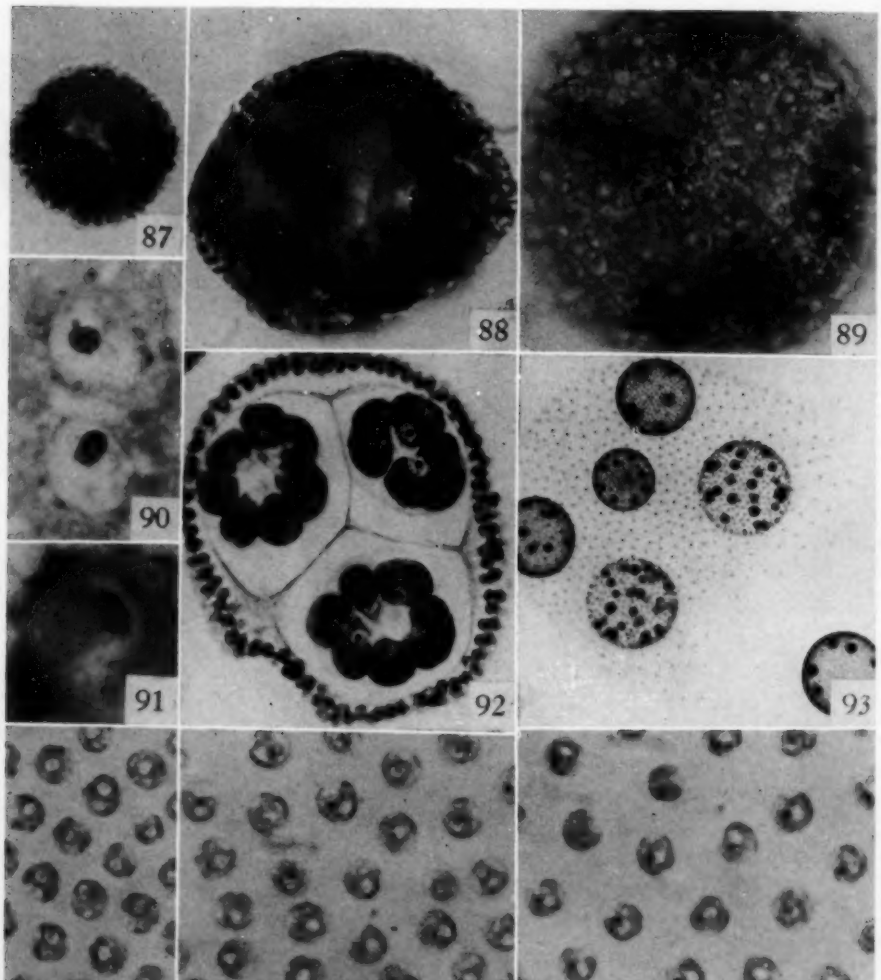
TABLE 1. *Data on Germination of Oospores.*

A Date of collection of material	B Date oospores placed in culture fluid	C Culture fluid	D State of oospores
27 My 41	7 Je 41	Moewus 10%	Wet
27 My 41	17 Jl 41	Moewus 10%	Wet
18 Jl 41	22 Jl 41	Moewus 10%	Wet
18 Jl 41	24 Jl 41	Moewus 10%	Wet
		Uspenski	Wet
18 Jl 41	25 Jl 41	Moewus 10%	Dry
		Uspenski	Dry
		Moewus (10%) + Uspenski (20%)	Dry
18 Jl 41	31 Jl 41	Moewus 10%	Wet
		Tricker's water	Wet
18 Jl 41	8 Jl 42	Tricker's water	Dry
6 Au 42	16 Au 42	Uspenski	Wet

E Date of germination	F Duration of rest period of oospores (days)	G Time required for germination (days)
9, 10 Je 41	12	3–4
18, 19, 20, 21 Jl 41	52	1–5
23 Jl 41	5	1–2
28 Jl 41	7	5
29 Jl 41	7	6
No germination	8	.....
" "	8	.....
" "	8	.....
4 Au 41	14	5
No germination	14	.....
No germination	1 year	.....
17 Au 42	11	1–2

With the aid of a binocular dissecting microscope, oospores in a minimum amount of fluid were drawn up into a thin pipette and transferred to a dish containing sterile culture fluid. Care was taken to exclude detritus and visible microorganisms. Spores were washed by several transfers into dishes containing fresh culture fluid. By this procedure contamination of the culture fluids was reduced to a minimum.

Petri dishes ($1\frac{1}{2}$–$2\frac{1}{2}$ inches in diameter) containing oospores and culture fluid were placed on glass shelves in a glass cabinet situated in front of a


87
88
89
90
91
92
93
94
95
96
97
98
99
100

window facing approximately north. Light from three 100-watt daylight bulbs, one on each side and one above, supplemented the daylight illumination during the day as well as at night.

All the stages of germination shown in the photographs (figs. 76–89) were derived from spores in Uspenski's fluid. The camera lucida drawings (figs. 22–30) illustrate germination stages of spores placed in Moewus' solution. The latter produced biflagellate zoospores and those in Uspenski's fluid yielded aplanospores. Either germination product, aplanospore or zoospore, gave rise, after successive divisions followed by inversion, to juvenile colonies (figs. 87–89). Obviously the conditions under which oospores were germinated in the laboratory differ somewhat from the conditions which obtain in nature. These experiments were not planned to determine the factors that control germination of the oospores, but rather were intended to induce germination so that successive stages could be observed and described.

An oospore about to germinate is easily recognized by its characteristic vesicular appearance (figs. 21, 76) apparently caused by the swelling of the mesospore which forces the protoplast to contract and become more dense.

A summary of the stages in the germination of an oospore follows: As stated above, oospores in Moewus' solution produce biflagellate zoospores, while those in Uspenski's fluid give rise to aplanospores. The history of the formation of aplanospores and zoospores is more or less the same, but for the development of a flagellar apparatus in the latter. Evidently, the swelling of the mesospore proceeds to such an extent that the exospore is

Explanation of figures 87–100

FIG. 87. Everted juvenile colony containing large reproductive cells. ×1400. FIG. 88. Optical section through juvenile colony. ×2400. FIG. 89. Surface view of a juvenile colony showing polygonal protoplasts containing numerous oil globules derived from the oospore. ×2400. FIG. 90. Two nuclei showing endosomes with buds attached; the endosome stains heavily and the bud less so. ×4800. FIG. 91. Anaphase of mitosis. This is the preparation from which figure 17 was prepared. Note the endosome lying outside of the spindle. ×4800. FIG. 92. Section through an asexual colony stained with methylene blue, showing the membrane structure. Note the thick prism membranes of the daughter colonies meeting near the center of the colony, and the colony membrane surrounding each daughter colony. ×1400. FIG. 93. Crushed mother colony containing four asexual daughter colonies and two male colonies. ×250. FIGS. 94–96 ×4800. FIG. 94. Protoplasts from posterior pole of a colony showing close proximity and lack of eyespots. FIG. 95. Protoplasts from the equatorial region of a colony; protoplasts more separated, some with small eyespots. FIG. 96. Protoplasts from the anterior pole of a colony; widely separated and all with large eyespots. FIG. 97. Surface view of a portion of a colony treated with methylene blue to show the membrane structure. × 2100. FIG. 98. Interphasic nucleus of a gonidium containing a large vacuolated endosome and a small plasmosome. ×4800. FIG. 99. Prophasic nucleus containing a divided endosome, the polar masses connected by granular threads. ×7500. FIG. 100. Nuclei at metaphase, illustrating synchrony of nuclear division in developing daughter colonies.

finally cracked by internal pressure; but other factors may be involved in the rupture. The mesospore projects through the cracked exospore (figs. 22, 76, 77) and continues to swell, thus widening the aperture (figs. 23, 78, 79, 80, 82) to permit finally the emergence of the entire mesospore together with its enclosed protoplast, leaving the empty exospore behind (figs. 24, 25, 80). When the contents of the spore have emerged about half-way (figs. 24, 25), a small clear beak or papilla develops at the anterior end of the protoplast and here soon afterward two short flagella are formed. These protrude through the endospore and wave feebly in the watery gelatinous substance of the mesospore. At this stage the endospore is clearly defined as a delicate membrane adhering closely to the anterior and posterior ends of the emerging protoplast but separated laterally (fig. 24). The greater part of the protoplast is extruded in about one hour; the remainder is discharged very rapidly. The liberated zoospore is distinctly *Chlamydomonas*-like, somewhat ellipsoidal, reddish-brown in color, with numerous oil globules and an anterior colorless beak from which two flagella project (fig. 25). While the zoospore moves slowly around by means of its flagella, it becomes somewhat enlarged and develops small green areas in the chloroplast. Finally, the flagella are lost and division begins.

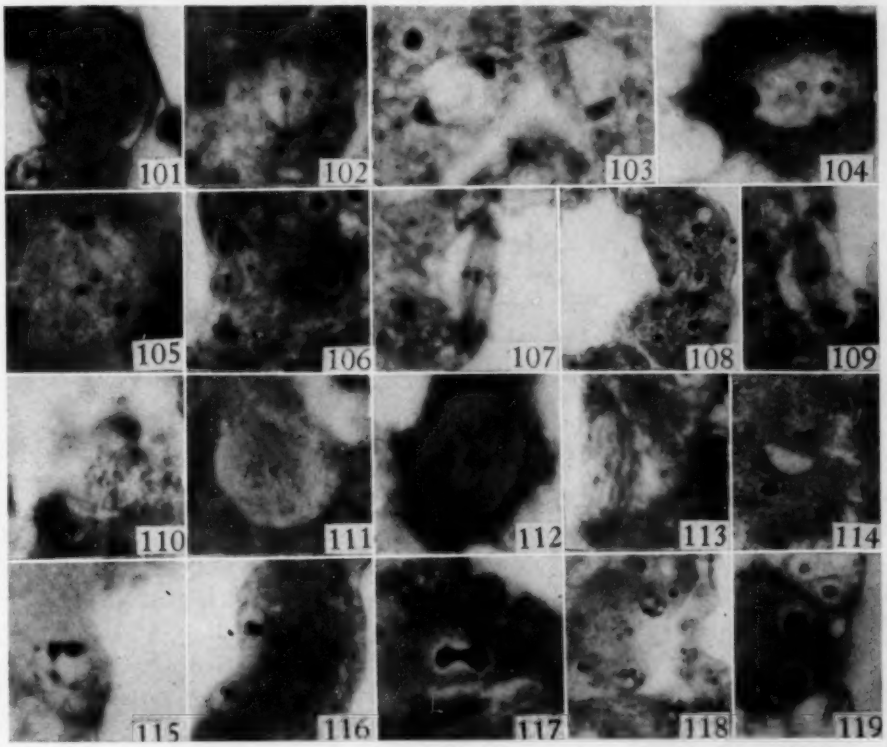
Liberated aplanospores are usually asymmetrical (fig. 81) but eventually become spherical (fig. 83), and then proceed to divide (figs. 84, 85). There is no sign of a flagellar apparatus nor is a beak formed.

The entire content of the oospore is given over to the formation of a single product, aplanospore or zoospore. On no occasion was there evidence of the formation of vestigial cells such as occur in the germination of oospores of *Eudorina* (Schreiber 1925) and which are believed to be suggestive of meiosis.

Each germinating oospore of *Volvox* generally contains a single nucleus which becomes incorporated into the germination products, aplanospore or zoospore. Infrequently, microtomed sections of germinating oospores reveal from two to four nuclei. Although about 100 germinating oospores were fixed at various stages and later sectioned and stained, there was no evidence of any meiotic activity except in the instances just mentioned.

From this point on, both oospore products have practically the same development. As division proceeds, the mesospore gradually becomes more and more hydrolyzed and finally disappears completely. After a few divisions (figs. 26–28), an irregular mass of cells, some of which are connected by distinct protoplasmic strands, is produced (fig. 29). Some distinctly larger cells (three or four) may be seen (fig. 86). These are the reproductive cells of the developing juvenile colony. Later the mass becomes oriented forming an irregular bowl with four indistinct lobes and three or four well differentiated, large reproductive cells, projected exteriorly (fig. 30). Inver-

sion then occurs and a motile juvenile colony is produced (fig. 87). This is scarcely larger than the original zoospore or aplanospore, since division proceeds rapidly with little, if any, growth. The colony is still rather brownish in appearance at this stage. A surface view reveals polygonal protoplasts



FIGS. 101–116. Intranuclear mitosis in vegetative cells of *V. Carteri* var. *Hazeni* involving endosomal division and extrusion. FIGS. 108 and 114 ×2400, others ×4800. FIG. 101. Interphase. FIGS. 102, 103. Division of the endosome. FIG. 104. Partial extrusion of a polar mass through the nuclear membrane. FIG. 105. Polar mass at top of nucleus and chromatic masses scattered throughout. FIG. 106. Chemical change occurring in a polar mass. The fingerlike portions within the nucleus stain deeply with nuclear dyes; the outer portions stain lightly or not at all. FIGS. 107–109. Metaphases-early anaphases with slight traces of polar masses visible. FIGS. 110–112. Anaphases; no trace of polar masses visible. FIGS. 113–115. Telophases. FIG. 116. Karyokinesis completed, cytokinesis beginning. FIG. 117. Division of a pyrenoid. ×4800. FIG. 118. Nuclear reorganization after nuclear division. ×2400. FIG. 119. Formation of massive endosomes in daughter nuclei. ×4800.

closely crowded together and containing numerous translucent oil globules (fig. 89). Their brownish color, small size, and oil globules sharply characterize young germ colonies. In optical section about four or five large reproductive cells, projecting into the interior, are visible (fig. 88).

Protoplasmic strands connect the cells throughout the development of a juvenile colony, even during inversion. Finally, prism walls are developed around the protoplasts, which gradually become rounded and greenish. During this process all protoplasmic connections disappear. The resultant juvenile colony is smaller and has fewer gonidia and vegetative cells than the vegetative *Volvox* colonies and differs in color. One or two, generally not all the gonidia in the juvenile colony undergo division and inversion and form asexual *Volvox* colonies. Pocock (1933) found that the daughters of juveniles were transitional between juveniles and the normal adults formed in succeeding generations.

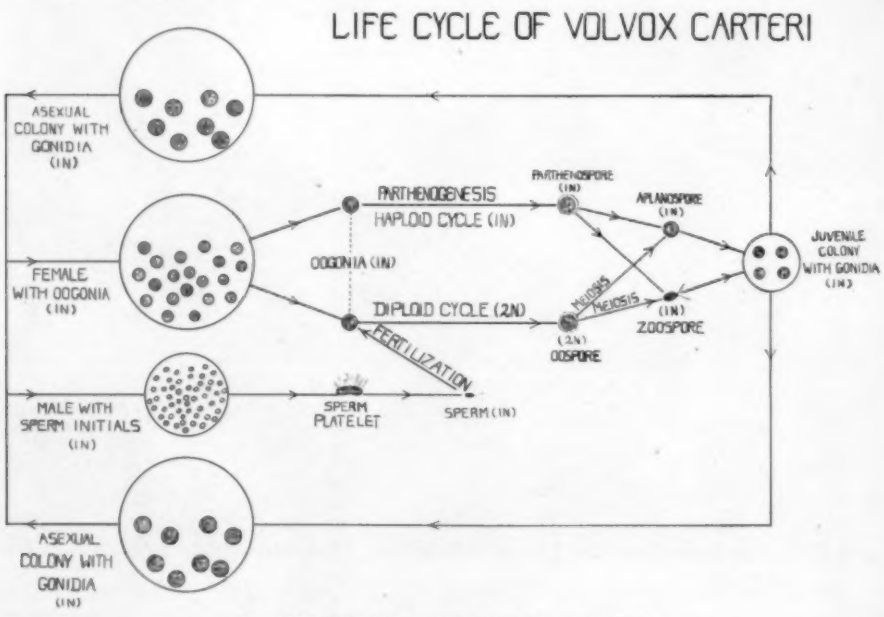


FIG. 120. The life cycle of *Volvox Carteri*.

In this study the formation of either aplanospores or zoospores was observed under different cultural conditions. Aplanospores were formed in synthetic medium (Uspenski & Uspenskaja 1925) and zoospores in soil extract (Moewus 1940). Other factors probably influence the development of the flagellar apparatus, but, undoubtedly, the medium in which the spores are germinated plays an important role. Pocock's conjecture (1933b) that parthenospores form aplanospores and oospores give rise to zoospores may be correct. Flagellated zoospores obtained in this study were produced by oospores which were isolated from the bottom of a general collection dish. Aplanospores were the products of oospores obtained from females which had been isolated from a general collection and had been allowed to mature

and release their eggs in separate culture dishes. This latter group had less opportunity for fertilization and thus parthenospores may have been formed, whereas in the former group prolonged association with other colonies provided greater opportunity for fertilization which would result in the formation of diploid oospores. At present, the evidence seems to indicate that environmental factors determine, at least to some extent, the production of aplanospores or zoospores in *V. Carteri*. Germination experiments show also that the period of ripening of oospores may be fairly brief. Ten days after healthy females were separated from a general collection, their released oospores were placed in Uspenski's fluid, where they germinated on the following day. Presumably, environmental conditions permitting, oospores ripen and germinate quickly in nature. Long resting periods may occur when oospores remain in unfavorable environments. In Zimmerman's (1921) cultures zygotes germinated after from two to three months, and were apparently unaffected by such external conditions as light and heat, although they were shielded, in part, from sunlight. Pocock (1933b) observed best germination from "oospores [of *V. Rousseletii*] placed in water obtained from *Volvox* 'vleis' [pools] and strained, placed in the sun," and "oospores placed in pond water plus a small quantity of culture medium (Uspenski and Uspenskaja 1925)." The later fluid used full strength "did not give good results, causing pathological phenomena in the developing colonies." The results of Pocock's (1933b) germination experiments on oospores of *V. Rousseletii* may be summarized as follows: 1. "Direct sunlight is necessary for the germination of the oospores." 2. "Complete drying is not essential but is beneficial." 3. "Oospores are not necessarily fully mature when liberated by the break up of the parent colony."

The present study of *V. Carteri* has shown that: (1) oospores may germinate under a combination of indirect daylight and artificial illumination; (2) only wet spores are capable of germination under the conditions provided in the experiments; (3) oospores mature and germinate rapidly (within two weeks) under conditions provided in the experiments; (4) either aplanospores or zoospores may be produced by germinating oospores according to the culture fluid used.

INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

The Index is reprinted monthly on cards, and furnished in this form to subscribers at the rate of three cents for each card. **The different subjects as classified below may now be ordered separately** (but no orders will be taken for less than one year's issue in any classification). Correspondence relating to the card issue should be addressed to the Treasurer of the Torrey Botanical Club.

PLANT TAXONOMY AND FLORISTICS
(exclusive of fungi)

(See also under Genetics: **Babcock**; under Ecology & Plant Geography: **Jones**)

Allard, H. A. The status of *Oxypolis rigidior* var. *ambigua* (Nutt). Robinson. Castanea **9**: 109, 110. *f. 1.* My–O[N] 1944.

Allard, H. A. & Leonard, E. C. Emandations to the papers of H. A. Allard and E. C. Leonard, "The Vegetation and Floristics of Bull Run Mountain, Virginia," Castanea 8. 1943, and "The Cladoniae of Bull Run Mountain, Virginia," Castanea IX, 1944. Castanea **9**: 119. My–O[N] 1944.

Anderson, E. Notes on variation in *Tithonia tubaeformis.* Ann. Mo. Bot. Gard. **31**: 239, 240. *f. 1.* 30 S 1944.

Baltzer, E. A. A monographic study of the genus *Palafoxia* and its immediate allies. Ann. Mo. Bot. Gard. **31**: 249–277. *pl. 10–13.* 30 S 1944.

Barkley, F. A. Schinus L. Brittonia **5**: 160–198. *f. 1–22.* 8 S 1944.

Batalla de Rodriquez, M. A. Contribucion al estudio de las gramineas del valle de Mexico, I. An. Inst. Biol. [Mexico] **15**: 17–25. *pl. 1, 2.* O 1944.

Beetle, A. A. The authorship of *Scirpus atrovirens.* Rhodora **46**: 336. 7 S 1944.

Beetle, A. A. A known but undescribed Mexican *Scirpus.* Brittonia **5**: 148. 8 S 1944.

Burkart, A. Las Leguminosas argentinas silvestres y cultivadas. *i–xix,* 1–590. *pl. 1–10, f. 1–123.* Buenos Aires, Acme Agency. 4 S 1943.

Clark, L. & Svihla, R. D. *Frullania brasiliensis.* Bryologist **47**: 108–112. *f. 1–34.* S 1944.

Core, E. L., Berkley, E. E. & Davis, H. A. West Virginia grasses. W. Va. Exp. Sta. Bull. 313: 1–96. *pl. 1–40.* My 1944.

Cory, V. L. *Forestiera* in southern and southwestern Texas. Madroño **7**: 252–255. 30 O 1944.

Covas, G. & Schnack, B. Tres nuevas especies de *Glandularia* de la flora argentina. Rev. Arg. Agron. **11**: 89–97. *f. 1–3.* Je 1944.

Croizat, L. Euphorbiaceae novae vel criticae columbianae, IV. Caldasia 11: 7–19. 20 Jl 1944.

Croizat, L. *Manihot Tweediana* Mueller is unacceptable. Rev. Arg. Agron. **11**: 173, 174. S 1944.

Croizat, L. Note sul genere *Julocroton* Martius. Rev. Arg. Agron. **11**: 98–102. Je 1944.

Croizat, L. One old and two new species of *Phyllanthus* from northwestern South America. Caldasia **11**: 21, 22. 20 Jl 1944.

Croizat, L. A study of the genus *Lophora* Coulter VII. The flower (part II). Desert **16**: 103–107. *f. 1–5.* S 1944.

Cronquist, A. Studies in the Simaroubaceae—IV. Resumé of the American genera. Brittonia **5**: 128–147. 8 S 1944.

Daily, F. K. The Characeae of Nebraska. Butler Univ. Bot. Stud. **6**: 149–171. *pl. 1–5.* 30 Au 1944.

Darrow, G. M. *et al.* Chromosome numbers in *Vaccinium* and related groups. Bull. Torrey Club **71**: 498–506. S 1944.

Dawson, E. Y. Some new Laurenciae from Southern California. Madroño **7**: 233–240. *pl. 26–28.* 30 O 1944.

Dore, W. G. White-flowered form of *Asclepias syriaca.* Rhodora **46**: 387, 388. O 1944.

Dugand, A. Noticias botanicias columbianas, III: especies nuevas y criticas. Caldasia 11: 33–38. *illustr.* 20 Jl 1944.

Epling, C. Supplementary notes on American Labiatae—III. Bull. Torrey Club **71**: 484–497. S 1944.

Ewan, J. Taxonomic history of perennial southwestern *Datura metaloides.* Rhodora **46**: 317–323. *pl. 838.* 7 S 1944.

Fassett, N. C. *Juniperus virginiana, J. horizontalis* and *J. scopulorum*—II. Hybrid swarms of *J. virginiana* and *J. scopulorum.* Bull. Torrey Club **71**: 475–483. *f. 1–6.* S 1944.

Fassett, N. C. Mass collections: *Equisetum sylvaticum.* Am. Fern Jour. **34**: 85–92. J–S 1944.

Fernald, M. L. The identities of *Epilobium lineare, E. densum* and *E. ciliatum.* Rhodora **46**: 377–386. O 1944.

Fernald, M. L. Is *Erigeron carolinianus* a valid American species? Rhodora **46**: 323–330. 7 S 1944.

Fernald, M. L. *Satureja vulgaris* (L.) Fritsch, var. *neogeae,* var. nov. Rhodora **46**: 388. O 1944.

Gilly, C. L. *Virola guatemalensis* (Hemsl.) Warb. in Mexico. Trop. Woods **79**: 5–8. 1 S 1944.

Green, I. J. An *Alopecurus* new to North America. Rhodora **46**: 386, 387. O 1944.

Heiser, C. H. Monograph of *Psilostrophe.* Ann. Mo. Bot. Gard. **31**: 279–301. *pl. 14.* 30 S 1944.

James, R. L. Some miscellaneous botanical observations. Castanea **9**: 111, 112. My–O [N] 1944.

Johnston, I. M. Plants of Coahuila, eastern Chihuahua, and adjoining Zacatecas and Durango, IV. Jour. Arnold Arb. **25**: 431–453. 16 O 1944.

Johnston, I. M. Publication-dates of Gaudichaud's Botany of the Voyage of the Bonite. Jour. Arnold Arb. **25**: 481–487. 16 O 1944.

Jones, C. H. Additions to the revised catalogue of Ohio vascular plants. XII. Ohio Jour. Sci. **44**: 188–191. Jl S 1944.

Kiener, W. Notes on distribution and bio-ecology of Characeae in Nebraska. Butler Univ. Stud. Bot. **6**: 131–148. 30 Au 1944.

Kühnemann, O. Géneros de briofitas de los alrededores de Buenos Aires. Lilloa **10**: 5–232. *f. 1–91, maps 1–12.* 31 Jl 1944.

Lee, L. W. Some bryophytes of Greenland. Bryologist **47**: 114–118. S. 1944.

Lemon, P. C. Two *Carices* new to Montana. Madroño **7**: 258. 30 O 1944.

Li, Hui-Lin The genus *Cedrela* in China. Trop. Woods 79: 16–24. 1 S 1944.

Li, Hui-Lin The phytogeographic divisions of China, with special reference to the Araliaceae. Proc. Acad. Nat. Sci. **96**: 249–277. 11 O 1944.

Lindsay, G. *Echinocereus subinermis.* Cactus & Succ. Jour. **16**: 134–136. *f. 122.* S 1944.

Little, E. L. Nomina conservanda proposals for ten genera of trees and shrubs. Madroño **7**: 240–251. 30 O 1944.

Looser, G. Sinopsis de los "*Asplenium*" (Filices) de Chile. Lilloa **10**: 233–264. *pl. 1–6. f. 1, 2.* 31 Jl 1944.

Lundell, C. L. *Cnidoscolus elasticus*, the source of highland Chilte, a remarkable new rubber yielding tree from the states of Durango and Sinaloa, Mexico. Field & Laboratory **12**: 33–38. Je 1944.

McInteer, B. B. Algae on wet rocks at Cumberland Falls State Park. Castanea **9**: 115, 116. M–O [N] 1944.

McInteer, B. B. Some noteworthy plants of Kentucky, II. Distribution of some "southern" species of trees and shrubs. Castanea **9**: 101–105. *f. 1, 2.* My–O [N] 1944.

McVaugh, R. The genus *Cnidoscolus:* generic limits and intrageneric groups. Bull. Torrey Club **71**: 457–474. S 1944.

Maguire, B. Great Basin plants—VIII. New Species in *Carex* and *Erigeron.* Brittonia **5**: 199–202. 8 S 1944.

Martinez, M. Nuevas especies de *Juniperus* Mexicanos. An. Inst. Biol. [Mexico] **15**: 7–15. *f. 1–8.* O 1944.

Martinez, M. Una nueva especie del genero *Pinus. Pinus michoacana.* An. Inst. Biol. [Mexico] **15**: 1–6. *f. 1–4.* O 1944.

Massey, A. B. The ferns and fern allies of Virginia. Bull. Va. Polytech. Inst. 37[7]: 1–110. *f. 1–21.* My 1944.

Massey, A. B. & Ball, C. R. The willows of Virginia. Bull. Va. Polytech. Inst. 37[9]: 1–31. Jl 1944.

Maxon, W. R. A new species of *Hemitelia* from Peru. Jour. Wash. Acad. **34**: 309, 310. 15 S 1944.

Miranda, F. Nuevos datos sobre *Euphorbia antisyphlitica* Zucc. An. Inst. Biol. [Mexico] **15**: 35–39. *f. 1.* O 1944.

Miranda, F. Tres nuevas gamopétalas del S. O. del estado de Puebla. An. Inst. Biol. [Mexico] **15**: 27–34. *f. 1–3.* O 1944.

Moldenke, H. N. Contributions to the flora of extra-tropical South America. V. Lilloa **10**: 285–362. 1 Jl 1944.

Moxley, E. A. Moss notes from Ontario. Bryologist **47**: 113. S 1944.

Ottley, A. M. The American *Loti* with special consideration of a proposed new section, *Simpeteria.* Brittonia **5**: 81–123. *f. 1–8.* 8 S 1944.

Record, S. J. Miscellaneous notes on tropical American woods. Trop. Woods 79: 1–5. 1 S 1944.

Rickett, H. W. *Cornus stolonifera* and *Cornus occidentalis.* Brittonia **5**: 149–159. *f. 1–3.* 8 S 1944.

St. John, H. Diagnoses of Hawaiian species of *Pelea* (Rutaceae) Hawaiian plant studies, 13. Lloydia **7**: 265–274. S 1944.

Sayre, G. Colorado species of *Grimmia.* Bryologist **47**: 118–122. S 1944.

Schnee, L. Las Ciperáceas del herbario nacional de Venezuela. Bol. Soc. Venez. Cien. Nat. 9[57]: 1–161. O–D 1943.

Schultes, R. E. Plantae columbianae, VIII. De distributione *Herraniae purpureae* notae. Caldasia 11: 23–32. *illust.* 20 Jl 1944.

Schweinfurth, C. An undescribed *Maxillaria* from the Peruvian highlands. Am. Orchid Soc. Bull. **13**: 130–132. *1 pl.* 1 S 1944.

Sealy, J. R. *Alstroemeria campaniflora.* Amaryllidaceae. Bot. Mag. **164**: *pl. 9664.* 24 Jl 1944.

Sharp, A. J. Notes on interesting bryophytes of the southern Appalachians, IV. Castanea **9**: 106–108. My–O [N] 1944.

Sharp, A. J. Some problems in American bryology. Lilloa **10**: 265–283. 31 Jl 1944.

Smith, C. P. Species *Lupinorum.* 417–432. Saratoga, Cal. Jl 1944. 418–448. Au 1944.

Standley, P. C. The status of the genus *Lecostemon* Moc. & Sesse. Trop. Woods 79: 9, 10. 1 S 1944.

Stewart, S. R. *Mentha arvensis* and some of its North American variations. Rhodora **46**: 331–335. 7 S 1944.

Svenson, H. K. The New World species of *Azolla.* Am. Fern Jour. **34**: 69–84. *pl. 6–8.* Jl–S [O] 1944.

Swallen, J. R. A new species of *Orcuttia* from Baja California. Jour. Wash. Acad. **34**: 308. 15 S 1944.

Torrey, R. E. *Modiola caroliniana* in Massachusetts. Rhodora **46**: 336. 7 S 1944.

Wagner, W. H. Two ferns new to Trinidad. Am. Fern Jour. **34**: 95, 96. Jl–S [O] 1944.

Weatherby, C. A. The group of *Selaginella oregana* in North America. Jour. Arnold Arb. **25**: 407–419. *pl. 1, 2.* 16 O 1944.

Wherry, E. T. *Cystopteris* Bluff. Am. Fern Jour. **34**: 92–94. Jl–S [O] 1944.

Wherry, E. T. *Osmunda cinnamomea* f. *cornucopiaefolia.* Am. Fern. Jour. **34**: 94, 95. Jl–S O 1944.

MORPHOLOGY

(including anatomy, and cytology in part)

Allard, H. A. *Cleistogamy* in *Lamium* (Labiatae). Castanea **9**: 112–114. My–O [N] 1944.

Allard, H. A. Second year sprouts of black cherry, *Prunus serotina,* fruiting. Castanea **9**: 117. My–O [N] 1944.

Bailey, I. W. The development of vessels in angiosperms and its significance in morphological research. Am. Jour. Bot. **31**: 421–428. *f. 1–9.* Jl [S] 1944.

Cornman, I. A summary of evidence in favor of the traction fiber in mitosis. Am. Nat. **78**: 410–432. S 1944.

Hsii, J. Structure and growth of the shoot apex of *Sinocalamus Beecheyana* McClure. Am. Jour. Bot. **31**: 404–411. *f. 1–18.* Jl [S] 1944.

Mousley, H. Peloria and other abnormalities in orchids. Canad. Field Nat. **58**: 73–76. *f. 1.* My–Je [S] 1944.

Sinnott, E. W. Cell polarity and the development of form in Cucurbit. Am. Jour. Bot. **31**: 388–391. *f. 1–10.* Jl [S] 1944.

Steil, W. N. *Leptosira mediciana* Borzi. Bull. Torrey Club **71**: 507–511. *f. 1–8.* S 1944.

Walker, R. I. Chromosome number, megasporogenesis, and development of embryo-sac of *Clintonia.* Bull. Torrey Club **71**: 529–535. *f. 1–37.* S 1944.

Wolf, F. A. & Jones, E. F. Comparative structure of green leaves of oriental tobacco at different levels on the stalk in relation to their quality upon curing. Bull. Torrey Club **71**: 512–528. *f. 1–5, t. 1–5.* S 1944.

PLANT PHYSIOLOGY

Currier, H. B. Water relations of root cells of *Beta vulgaris*. Am. Jour. Bot. **31**: 378–387. *f. 1.* Jl [8] 1944.

Justice, O. L. Viability and dormancy in seeds of *Polygonum amphibium* L., *P. coccineum* Muhl., and *P. hydropiperoides* Michx. Am. Jour. Bot. **31**: 369–377. *f. 1–3.* Jl [8] 1944.

Kelly, S. Effect of different concentrations of synthetic auxins on decapitated sunflower stems. Bull. Torrey Club **71**: 549–554. *f. 1–3, t. 1, 2.* S 1944.

Kramer, P. J. Soil moisture in relation to plant growth. Bot. Rev. **10**: 525–559. N 1944.

Pratt, R. Studies on *Chlorella vulgaris*. IX. Influence on growth of *Chlorella* of continuous removal of chlorellin from the culture solution. Am. Jour. Bot. **31**: 418–421. *f. 1.* Jl [8] 1944.

Smock, R. M. The physiology of deciduous fruits in storage. Bot. Rev. **10**: 560–598. N 1944.

Steinitz, L. M. The effect of lack of oxygen on meiosis in *Tradescantia*. Am. Jour. Bot. **31**: 428–443. *pl. 1, 3.* Jl [8] 1944.

GENETICS
(including cytogenetics)

Babcock, E. B. New light on evolution from research on the genus *Crepis*. Am. Nat. **78**: 385–409. *f. 1–5.* S 1944.

Faberge, A. C. Genetics of the *Scapiflora* section of *Papaver*. III. Interspecific hybrids and genetic homology. Jour. Genet. **46**: 125–149. Ap 1944.

Whaley, W. G. Heterosis. Bot. Rev. **10**: 461–498. O 1944.

MYCOLOGY AND PHYTOPATHOLOGY

Arndt, C. H. Infection of cotton seedlings by *Colletotrichum gossypii* as affected by temperature. Phytopathology **34**: 861–869. *f. 1–3.* O 1944.

Bennett, C. W. Studies of dodder transmission of plant viruses. Phytopathology **34**: 905–932. *f. 1–3* O 1944.

Bitancourt, A. A. Distribuição teórica de lesões em folhas ou frutas, causadas por insetos e outros animais ou por agentes infecciosos transmitidos por vetores. Arq. Inst. Biol. [São Paulo] **14**: 243–252. D 1943.

Bliss, D. E. A new species of *Alternaria* on fruit of *Phoenix dactylifera*. Mycologia **36**: 538–549. *f. 1, 2.* S–O 1944.

Bliss, D. E. & Fawcett, H. S. The morphology and taxonomy of *Alternaria Citri*. Mycologia **36**: 469–502. *f. 1–5.* S–O 1944.

Dix, W. L. *Cetraria islandica* in Pennsylvania. Bryologist **47**: 129, 130. S 1944.

Dodge, B. O. A new *Pseudonectria* on *Pachysandra*. Mycologia **36**: 532–537. *f. 1–13.* S–O 1944.

Edgerton, C. W. & Carvajal, F. Host-parasite relations in red rot of sugarcane. Phytopathology **34**: 827–837. *f. 1–6.* S 1944.

Edmonson, C. H. Note on resistance of species of *Antidesma* to marine borers. Trop. Woods **79**: 15. 1 S 1944.

Hart, H. Stem rust on new wheat varieties and hybrids. Phytopathology **34**: 884–899. *f. 1–4.* O 1944.

Herre, A. W. C. T. On a small collection of lichens from San Miguel County, New Mexico. Bryologist **47**: 131–134. S 1944.

Jenkins, A. E. A recent account of anthracnose of poplar in Italy. Rev. Arg. Agron. **11**: 103–105. *pl. 11.* Je 1944.

Johanson, A. E. An endo-operculate chytridiaceous fungus: *Karlingia rosea* gen. nov. Am. Jour. Bot. **31**: 397–403. *f. 1–37.* Jl [8] 1944.

Jones, F. R. Life history of *Cercospora* on sweetclover. Mycologia **36**: 518–525. S–O 1944.

Kanouse, B. B. A new discomycete from the Olympic National Forest. Mycologia **36**: 460–463. S–O 1944.

Karling, J. S. Brazilian anisochytrids. Am. Jour. Bot. **31**: 391–397. *f. 1–64.* Jl [8] 1944.

Kern, F. D. & Thurston, H. W. Additions to the Uredinales of Venezuela—IV. Mycologia **36**: 503–517. S–O 1944.

Linder, D. H. A new rust of orchids. Mycologia **36**: 464–468. *f. 1–8.* S–O 1944.

McKinney, H. H. Descriptions and revisions of several species of viruses in the genera *Marmor, Fractilinea,* and *Galla.* Jour. Wash. Acad. **34**: 322–329. 15 O 1944.

McLean, D. M. Histo-pathologic changes in the phloem of American elm affected with the virus causing phloem necrosis. Phytopathology **34**: 818–826. *f. 1–3.* S 1944.

Martinez Crovetto R. Algunos casos teratologicos en gramineas. Rev. Arg. Agron. **11**: 106–115. *f. 1–7.* Je 1944.

Orejuela, C. G. New or heretofore unreported species of the higher ascomycetes from Colombia and Venezuela. Mycologia **36**: 429–459. S–O 1944.

Rudolph, B. A. & Harrison, G. J. The unimportance of cotton seed in the dissemination of *Verticillium* wilt in California. Phytopathology **34**: 849–860. *f. 1.* O 1944.

Semeniuk, G. Seedling infection of dent maize by *Sclerotium bataticola* Taub. Phytopathology **34**: 838–843. *f. 1.* S 1944.

Shanor, L. Additional records of aquatic Phycomycetes isolated from Mexican soils. Jour. Wash. Acad. **34**: 330–333. 15 O 1944.

Silberschmidt, K. Estudios sôbre a transmissão experimental da "clorose infecciosa" das Malváceas. Arq. Inst. Biol. [São Paulo] **14**: 105–156. *pl. 11–17.* D 1943.

Simonds, A. O. & Kreutzer, W. A. Infection phenomena in tomato-fruit rot caused by *Phytophthora capsici.* Phytopathology **34**: 813–817. *f. 1, 2.* S 1944.

Singer, R. On some Basidiomycetes new for the United States. Mycologia **34**: 552–554. S–O 1944.

Smith, A. H. New and interesting *Cortinarii* from North America. Lloydia **7**: 163–235. *pl. 1–10.* S 1944.

Thompson, R. C. *et al.* Investigations on the transmission of big vein of lettuce. Phytopathology **34**: 900–904. O 1944.

Thomson, J. W. Some lichens from central Pennsylvania. Bryologist **47**: 122–129. S 1944.

ECOLOGY AND PLANT GEOGRAPHY

Cormack, R. G. H. The effect of environmental factors on the development of root hairs in *Phleum pratense* and *Sporobolus cryptandrus.* Am. Jour. Bot. **31**: 443–449. *f. 1–11.* Jl [8] 1944.

Dansereau, P. Les érablières de la Gaspésie et les fluctations du climat. Contr. Inst. Bot. Univ. Montreal **51**: 1–18. *f. 1.* 1944.

Friesner, R. C. & Ek, C. M. Correlation of microclimatic factors with species distribution in Shenk's Woods, Howard County, Indiana. Butler Univ. Bot. Stud. **6**: 87–101. 30 Au 1944.

Friesner, R. C. & Potzger, J. E. Survival of hemlock seedlings in a relict colony under forest conditions. Butler Univ. Bot. Stud. **6**: 102–115. 30 Au 1944.

Jones, C. H. Studies in Ohio floristics—III. Vegetation of Ohio prairies. Bull. Torrey Club **71**: 536–548. *f. 1–5*. S 1944.

PALEOBOTANY

Potzger, J. E. Pollen frequency of *Abies* and *Picea* in peat: a correction on some published records from Indiana bogs and lakes. Butler Univ. Bot. Stud. **6**: 123–130. 30 Au 1944.

Wilson, L. R. Spores and pollen as microfossils. Bot. Rev. **10**: 499–523. O 1944.

GENERAL BOTANY
(including biography)

Barnhart, J. H. Dates of the "Bryologia Europaea." Bryologist **47**: 97–108. S 1944.

Bartholomew, E. A. A. B. Brooks. Castanea 9: 117, 118. My–O [N] 1944.

B[enedict] R. C. Hubert Earl Ransier. Am. Fern Jour. **34**: 99, 100. Jl–S [O] 1944.

Brunel, J. Les grandes étapes de l'algologie Americaine. Contr. Inst. Bot. Univ. Montreal **52**: 1–32. *f. 1–8*. 1944.

Cook, O. F. Natural rubber. Ann. Rept. Smithsonian Inst. **1943**: 363–411. *pl. 1–20*. 1944.

Correll, D. S. Vanilla: its history, cultivation and importance. Lloydia **7**: 236–264. *f. 1–4*. S 1944.

Gagnon, A. Le Frère Marie-Victorin. Nat. Canad. **71**: 172–175. *port.* Jl–Au 1944.

Morris, H. E. & Cotner, F. B. Deane B. Swingle 1879–1944. Phytopathology **34**: 769–771. *port.* S 1944.

Muenscher, W. C. Aquatic plants of the United States. *i–x*, 1–374. *f. 1–154*. Ithaca, N. Y., Comstock Pub. Co., 1944.

Nishimura, M. S. *et al.* The propagation of guayule from cuttings. Am. Jour. Bot. **31**: 412–418. *f. 1–6*. Jl [8] 1944.

Roche e Silva, M. Estudios sôbre plantas tóxicas no estado de São Paulo. Ensaios toxicológicas com 27 plantas consideradas "suspeitas." Arq. Inst. Biol. [São Paulo] **14**: 15–30. *pl. 5–7*. S 1943.

Rogers, D. P. On the dates of publication of Schweinitz's *Synopses*. Mycologia **36**: 526–531. S–O 1944.

Walker, E. H. The plants of China and their usefulness to man. Ann. Rept. Smithsonian Inst. **1943**: 325–361. *pl. 1–12*. 1944.